

Morphological differences in a population of Rufous-collared Sparrow (*Zonotrichia capensis*, Statius Müller, 1776) (Passerine, Emberizidae) at different elevations in the Tropical Andes

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Abstract: Populations that breed along steep elevation gradients show diverse physiological and morphological changes in response to the different environmental conditions. The latter has been discussed by Bergmann's and Allen's ecogeographic rules about body and appendage sizes and environmental temperature. We compared morphometric measures (mass, bill width, tarsus, wing, and tail length) of a *Zonotrichia capensis* population in two localities at different elevations with similar latitudes and photoperiods on the western slope of the Colombian Central Andes. We compared a Low Elevation locality (LE) at 1800 m a.s.l. and a High Elevation locality (HE) at 3853 m a.s.l. that have approximate wind speeds of 1.3 m/s and 8.4 m/s, respectively. During 12 months of sampling, we captured 46 adults using mist-nets; 26 in the LE and 20 in the HE. Each individual was sexed using molecular techniques at the Laboratory of Genetics of the Department of Biological Sciences of Universidad de Caldas. Individuals (males + females) from the HE had longer wings and tails than those from the LE ($F_{1,44} = 5.93$; $P = 0.019$). Also, wings of males in the HE were longer than those of females in both localities and tails of males in the HE were longer than those of LE males. Our results did not agree with what was expected according to Allen's and Bergmann's ecogeographic rules. Longer wings and tails increase sustainment, maneuverability, and balance in low atmospheric pressures and strong air currents and these conditions are found at high elevation habitats. Most likely, the longer wings found for HE males allow greater movement during territorial behavior. Further, these differences in morphological traits along elevational gradients could result from micro-evolutionary changes between localities or phenotypic plasticity of individuals exposed to different environmental conditions.

Keywords: wing length, tail length, adaptive traits, paramo, territory, ecogeographic rules

Diferencias morfológicas en una población de Copetón (*Zonotrichia capensis*, Emberizidae) a diferente altitud en los Andes tropicales.

Resumen: Las poblaciones que se reproducen en gradientes altitudinales, adoptan diversos cambios morfológicos para afrontar las condiciones ambientales. En el presente estudio se compararon las medidas morfológicas (peso corporal, longitud del tarso, ala, cola y culmen) de una población de *Zonotrichia capensis*, a diferente altitud en los Andes colombianos. Las localidades de tierra baja (TB) y alta (TA) se encuentran a 1800 m.s.n.m. y 3853 m.s.n.m., con velocidad aproximada del viento de 1.3 m/s y 8.4 m/s, respectivamente. Durante 12 meses se realizó la captura de 46 individuos (TB n=26, TA n=20) para la medición de los rasgos morfológicos. La longitud del ala de los individuos de TA fue mayor que en TB. Así mismo, en machos de TA la longitud del ala fue mayor que en hembras en general. Es posible que a las más grandes incrementen la eficiencia del vuelo en zonas ventosas y con baja presión atmosférica, como ocurre en TA. Probablemente la diferencia del tamaño del ala entre los machos de TA y las hembras, se deba a un mayor desplazamiento dentro de la conducta territorial. Estas diferencias podrían ser el resultado de cambios microevolutivos entre localidades o la plasticidad fenotípica de individuos expuestos a diferentes condiciones ambientales.

Palabras clave: Longitud del ala, longitud de cola, rasgos adaptativos, páramo, territorial, reglas ecogeográficas.

Introduction

Ecogeographic variations in the morphometry of bird populations have been associated with climatic, latitudinal, and elevational factors (Aldrich & James 1991, Blackburn & Ruggiero 2001). In particular, two of the most important ecogeographic principles in Bergmann's and Allen's rules relate to thermoregulation (Mayr 1970). Bergmann's rule suggests that smaller individuals are found in warmer parts of a species' range and larger individuals are located in cooler regions (Bergmann 1847). Further, Allen's rule suggests that the size of the appendages (e.g., bill, wings, and limbs) are relatively shorter in colder environments (Allen 1877). The usual explanation for these ecogeographic rules concerns the need for organisms to prevent or promote heat dissipation (Blackburn *et al.* 1999). For instance, large animals with smaller extremities expend less energy in thermoregulation because of their smaller surface to volume ratio. This has been a reference framework to explain the morphological differences between bird populations exposed to different environmental conditions (Gutierrez-Pinto *et al.* 2014, Sun *et al.* 2016, Blackburn *et al.* 1999). However, other environmental factors besides temperature have been proposed to contribute to geographic variations in body size, such as humidity, primary productivity, seasonality, and resource availability (Meiri *et al.* 2007, Graves 1991, Guillaumet *et al.* 2008, James 1970). Environmental changes resulting from elevational gradients have been associated with variations in morphological traits between bird populations, as well as between sexes. These such traits include body mass, plumage color, wing length, tail, peak, among others (Landmann & Winding 1995, Bears *et al.* 2008, Blackburn & Ruggiero 2001, Graves 1985, Price 1991). In this regard, morphological differences between sexes have been explained by differences in foraging behavior, territoriality, courtship, and escape (Landmann & Winding 1993, Bears *et al.* 2008, Fisher *et al.* 2004). It is suggested that each sex can respond differently regarding behavior and morphology with altitude (Bears *et al.* 2009, Zammuto & Millar 1985).

Although the greatest bird diversity is concentrated in the Tropics and many of these species have populations distributed along a broad altitudinal range (Rising *et al.* 2010, Ghalambor *et al.* 2014, Tarlow *et al.* 2001), there are few studies in the region that show morphological variations in bird populations in response to elevation (Caro *et al.* 2013, Gutierrez-Pinto *et al.* 2014, Blackburn & Ruggiero 2001, Traylor 1950). This limits the formulation of hypotheses about the contribution of environmental factors in elevational gradients to the evolution of populations at a micro-evolutionary scale. This can be a key approach to understanding the diversification patterns that occurred in the Andes. Especially, in middle elevations where birds are more diverse and it is suggested that speciation rates are higher (Kattan & Franco 2004). Additionally, understanding morphological or phenotypical variation with elevation can provide insight into how animals adapt to their current environment. Finally, studying bird adaptations to elevational gradients may also aid in predicting the outcomes of climate change (Báez *et al.* 2016).

The Rufous-collared Sparrow (*Zonotrichia capensis* Statius Müller, 1776) (Passerine, Emberizidae) has one of the largest distributions of any Neotropical passerine, from southern Mexico to Cape Horn, Chile. Its extensive distribution spans a multitude of environments and a variety of habitats, such as coastal, paramo, humid forest, and urban areas, from lowlands, at sea level, to highland areas (4600 m a.s.l.) (Rising *et al.* 2010, Chapman 1940).

This makes the Rufous-collared Sparrow a suitable species to address questions associated with adaptation to contrasting environmental conditions. *Z. capensis* is a socially monogamous species, with a monomorphic plumage and aggressive territorial defense by males during the reproductive season (Rising *et al.* 2010, Miller & Miller 1968, Moore *et al.* 2002). These features, combined with recognized morphologic differences between subspecies and differences in behavior, vocalization, and life-history traits between and within populations throughout the distribution range (Cardona *et al.* 2017, Danner *et al.* 2011, Handford 1985), makes it an ideal study organism. This study identified the morphological changes in a *Z. capensis costaricensis* non-migratory population at different elevations in the Colombian Central Andes. Since morphological traits in birds can vary due to environmental factors related to elevation and considering that *Z. capensis* displays differences in its physiology and life-history traits with elevation, we expected that, according to the ecogeographic rules of Bergman or Allen, individuals that live at higher elevations will have a larger body size and smaller appendages size.

Materials and methods

In the Colombian Central Andes, the Rufous-collared Sparrow is present between 1000 and 3700 m a.s.l. (Hilty *et al.* 2001). The population has three reproductive peaks throughout the year and there is an evident reduction in clutch size with an increase in altitude in the Central Andes (Cardona *et al.* 2017). Pairs stay in the territory year-round and territorial behavior shown by males only during the breeding season, which includes territorial songs, flights towards the intruder, approaching and attacking the intruder, and spending extended periods close to the intruder (Miller & Miller 1968, Moore *et al.* 2002). Additionally, juveniles differ from adults in plumage characteristics (Miller & Miller 1968).

1. Study site

To compare the morphology of *Z. capensis* at different elevations, we selected two localities situated on a continuum without geographical barriers, with similar latitudes and photoperiods on the western slope of the Colombian Central Andes. Both localities are part of the Chinchiná River basin in the department of Caldas. In this study site, it is possible to find individuals of the species throughout the altitudinal gradient between the two localities. The region has a bimodal precipitation pattern, with the greatest amount of rainfall occurring during April-May and October-November, whereas minor rainfall concerning the annual average rainfall takes place in June-September and December-March (Morales *et al.* 2012). The localities differ in elevation by 2000 m and are separated in a straight line by 26 km. The high elevation locality (HE) is located in the *vereda* La Laguna (4°58'49.3"N - 75°20'06.8"W; 3853 m a.s.l.), in the paramo region, with an average annual temperature of 7.1 °C (min. 4.4 °C and max. 10.3 °C), annual rainfall of 1848 mm (Cenicafé & FNC 2016) and average annual wind speed of 4.1 m/s (Cárdenas 2016). The HE locality was covered by a glacier during the Pleistocene approximately 10,000 years ago (Thouret *et al.* 1997). The Low elevation locality (LE) is located in the *vereda* Alto del Naranjo (5°00'29.8"N - 75°33'41.2"W; 1800 m a.s.l.) in the coffee region, with an average annual temperature of 20.7 °C (min. 16.8 °C and max. 26.3 °C), annual rainfall of 2817 mm (Cenicafé & FNC 2016), and approximate average annual wind speed of 1.3m/s (Baldi & Guzm 1998).

2. Capture procedures, morphometric measurements, and blood sampling

For bird capture, we used five mist-nets (12 x 2.5 m x 36 mm) and obtained a total capturing effort of 1120 and 1680 hours net⁻¹ for the LE and HE localities, respectively, from December 2015 to December 2016. The captured birds were marked using bands with a unique color combination for later identification and released at the same capturing place. Five morphometric measurements were registered for the adult individuals, including wing chord and tail lengths using an ornithological ruler (± 0.5 mm); bill length from the base, tarsus length using a digital caliper (± 0.03 mm), and mass using a scale (± 1 g). All measurements were performed by the same investigator. For sex determination of the captured birds, we collected a drop of blood obtained by brachial venipuncture (Quirici *et al.* 2014) and the blood was stored in an FTA classic card (Whatman®).

3. Molecular sexing

The sex determination of the individuals was performed by molecular techniques. DNA extraction was performed using the DNeasy Blood and Tissue kit (Qiagen®), following the manufacturer's protocol. Subsequently, we performed PCR amplification of the conserved flanking regions (exons) and non-conserved regions (introns) of the *chd* (chromodomainhelicase-DNA-binding protein) gene, which is present on both sex chromosomes (Z and W) and allows differentiating females (*chd*-ZW) from males (*chd*-ZZ). The regions were amplified using primers P2 (5'-TCTGCATCGC-TAAATCCTT-3') and P8 (5'-CTCCCAAGGATGAGRAAYTG-3') (Griffiths *et al.* 1998). PCR was performed on a Techne TC-PLUS thermocycler, according to the following conditions: initial denaturation at 95°C for 5 min, followed by 5 cycles at 94 °C for 40 s, 55 °C for 40 s, and 72 °C for 55 s; subsequently, 30 cycles at 94°C for 30 s, 48 °C for 30 s, and 72 °C for 45 s, completing the reaction with a final extension cycle at 72 °C for 5 min. The PCR products were visualized on horizontal 3% agarose gels with 1X TBE pH 8.0 running buffer at 70 volts (for 6 hours), stained with SYBR Safe® dye and photo-documented on a GelDoc-It®2 310 Imager (UVP). The birds were identified as females when two bands were present or as males when an exclusive band was observed. The molecular analyses were performed at the Laboratory of Genetics of the Department of Biological Sciences (Faculty of Exact and Natural Sciences) of Universidad de Caldas (Colombia).

The morphometric traits between the localities were compared by two-way analyses of variance (ANOVAs) (Zar 1996), after assessing goodness-of-fit to a normal distribution and homogeneity of variances through Shapiro-Wilk and Levene tests, respectively. The morphometric traits between sexes, as well as between and within localities, were compared using a Tukey *post hoc* test (Zar 1996). Pairwise correlations between the morphometric traits were determined through Pearson's correlation coefficient. These analyses were performed using R version 3.3.1 (R Core Team. 2016).

Results

We captured 46 adults, specifically, 20 and 26 in HE and LE localities, respectively. Molecular sexing showed 14 males for each locality and 6 females (HE) and 12 females (LE). Individuals (males + females) from HE had on average 3.4% longer wings than LE individuals ($F_{1,44} = 5.93$; $P = 0.019$, Figura 1.A). Likewise, tail length was on average 4.3% longer in HE locality than LE locality ($F_{1,41} = 5.79$; $P = 0.02$, Figura 1.B). We found no significant differences between localities for morphometric measures such as bill length ($F_{1,41} = 1.38$; $P = 0.05$), tarsus length ($F_{1,43} = 0.979$; $P = 0.328$), and mass ($F_{1,42} = 1.084$; $P = 0.3$). Similarly, these measures do not show significant differences between sexes ($P > 0.05$). The comparison of the morphometric traits between sexes and between and within localities shows that males from HE had longer wings than females from both localities, on average 6.2% and 7.2% longer compared to HE and LE females, respectively (Tukey HSD, $P = 0.015$; and $P < 0.01$, respectively, Figura 1.C). Likewise, HE males had longer tails than LE males (Tukey HSD, $P = 0.019$, Figura 1.D). Moreover, we did not find a correlation between morphometric traits such as mass and wing length ($r = 0.27$; $P = 0.07$), mass and tail length ($r = 0.30$; $P > 0.05$), or wing and tail length ($r = 0.27$; $P = 0.08$).

Discussion

Our results did not agree with what was expected according to Allen's and Bergmann's ecogeographic rules. Conversely, the length of the appendages, in this case, the wings and tails, was greater in the highland individuals. Differences in flight-related morphologic structures among birds at different elevations have been observed in populations of passerines from temperate regions, including *Junco hyemalis* (Bears *et al.* 2008) and *Passer montanus* (Sun *et al.* 2016). These studies suggest that the longer length in flight structures (wing and tail) at high elevations is associated with low atmospheric pressure and strong wind speed. Longer wings and tails help to increase flight efficiency, maneuverability, as well as balance and lift in conditions of high elevation (Landmann & Winding 1993, Altshuler & Dudley 2006, Maybury & Rayner 2001). Likewise, morphometric differences in wings between males from HE and females from both localities may be due to the territorial behavior of males of *Z. capensis*, similar to other species such as the dark-eyed junco (*J. hyemalis*) in western Canada and the henna-capped foliage-gleaner (*Clibanornis rectirostris*) in southeastern Brazil (Faria *et al.* 2007, Bears *et al.* 2008). Most likely, territorial behavior under windy conditions, such as those found in HE locality, could lead to more efforts in flight displacement to maintain and defend the territory. Thus, longer wings can be beneficial to maneuverability and greater displacement of males under conditions of high elevation (Landmann & Winding 1993, Bears *et al.* 2008, Fisher *et al.* 2004).

Differences in morphological traits between individuals along elevational gradients could reflect the strong selection imposed by local environmental conditions. These morphological differences can result from micro-evolutionary changes during the process of local adaptation of populations or phenotypic plasticity of individuals exposed to different environmental conditions. It is possible that in the Tropical Andes, climatic shifts related to global climate change can alter species local adaptation processes throughout their distribution ranges (Gardner *et al.* 2014, Goodman *et al.* 2012).

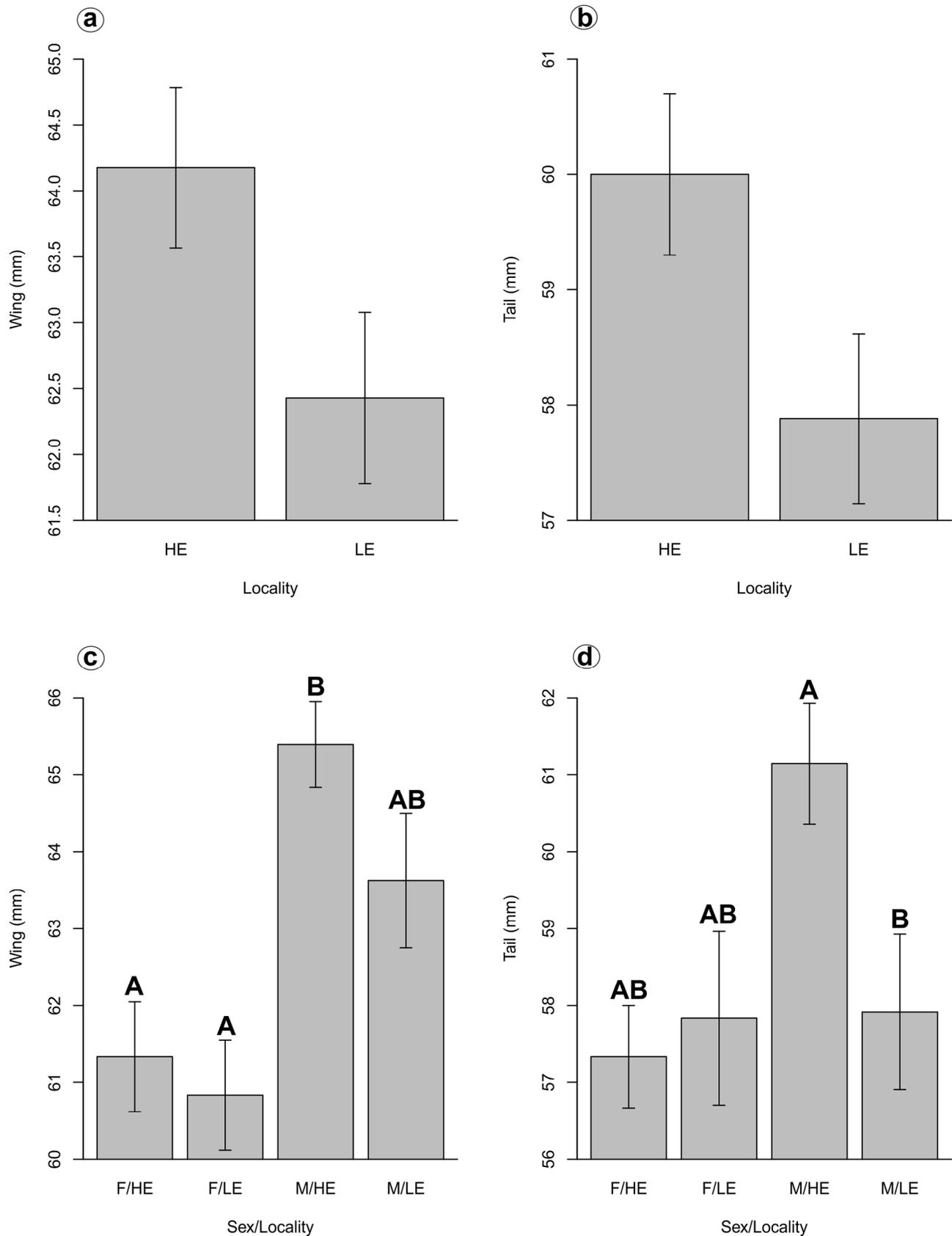


Figure 1. Morphology of *Z. capensis* in the Central Andes, Colombia. Comparison of morphological traits. There were significant differences between localities in (A) wing length and (B) tail length (male + female). Likewise, there were significant morphological differences between sexes (female: F and, male: M), between and within localities in (C) wing length, males from HE had longer wings than females from both localities, and (D) in tail length, between HE and LE males. Different letters above the bars indicate significant differences ($P < 0.05$).

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Author contributions

Ana Busi (Corresponding Author) performed a substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation and; contribution to manuscript preparation.

Leydy J. Cardona-Salazar performed a contribution to data collection.

Daniela Gómez Castillo performed a contribution to data collection.

Paula A. Ossa-López performed a contribution to data analysis and interpretation; contribution to manuscript preparation.

Fredy A. Rivera-Páez performed contribution to manuscript preparation; contribution to data analysis and interpretation.

Rodrigo A. Vásquez performed a contribution to critical revision, adding intellectual content.

Gabriel J. Castaño-Villa performed a substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to manuscript preparation and; contribution to critical revision, adding intellectual content

Conflicts of interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

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