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Altitudinal morphometric variation in Rufous-collared Sparrow *Zonotrichia capensis* (Aves: Passerellidae) in the southwestern Peruvian Andes

Variación morfométrica altitudinal en el gorrión de collar rufo *Zonotrichia capensis* (Aves: Passerellidae) en el suroeste de los Andes peruanos

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Abstract

Ecogeographic rules such as Bergmann's and Allen's provide a framework to evaluate how morphological traits vary across environmental gradients. We tested these rules in the Rufous-collared Sparrow (*Zonotrichia capensis*), a broadly distributed Neotropical passerine, along an altitudinal gradient in southwestern Peru. We conducted morphometric analysis on 192 individuals from 16 localities distributed across two river basins in the Arequipa region, covering elevations from sea level to 3800 m. Seven morphological traits were measured, including body mass (to test Bergmann's rule) and appendages such as bill length, width, and height, wing length, tarsus length, and tail length (to assess Allen's rule). Generalized linear mixed models were used to evaluate the effects of sex, elevation, and river basin. Our results support Bergmann's rule but provided only partial support for Allen's rule—bill length decreased with elevation, while other appendages showed no clear pattern or

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exhibited trends opposite to classical predictions. Additionally, males exhibited larger body size and longer bills than females. These findings suggest that *Z. capensis* populations exhibit complementarity between ecogeographical rules, and altitude-associated morphological variation consistent with thermoregulatory expectations, although non-thermal ecological and biological factors may also shape phenotypic diversity across elevations.

Keywords: Bergmann's rule, Allen's rule, phenotypic variation, altitudinal gradient, Andean birds.

Resumen

Las reglas ecogeográficas, como las de Bergmann y Allen, proporcionan un marco para evaluar cómo varían los rasgos morfológicos a lo largo de gradientes ambientales. Probamos estas reglas en el gorrión de collar rufo (*Zonotrichia capensis*), un paseriforme neotropical ampliamente distribuido, a lo largo de un gradiente altitudinal en el suroeste de Perú. Realizamos un análisis morfométrico de 192 individuos de 16 localidades distribuidas a lo largo de dos cuencas en la región de Arequipa, que abarcaban altitudes desde el nivel del mar hasta los 3800 m. Se midieron siete rasgos morfológicos, incluyendo la masa corporal (para probar la regla de Bergmann) y apéndices como la longitud, anchura y altura del pico, longitud del ala, longitud del tarso y longitud de la cola (para evaluar la regla de Allen). Se utilizaron modelos lineales mixtos generalizados para evaluar los efectos de sexo, altitud y cuenca hidrográfica. Nuestros resultados respaldaron la regla de Bergmann más solo un apoyo parcial a la regla de Allen: la longitud del pico disminuyó con la altitud, mientras que los otros apéndices no mostraron un patrón claro o exhibieron tendencias opuestas a las predicciones clásicas. Además, los machos presentaban un tamaño corporal mayor y picos más largos que las hembras. Estos hallazgos sugieren que las poblaciones de *Z. capensis* muestran una complementariedad entre las reglas, además de una variación morfológica asociada a la altitud coherente con las expectativas termorreguladoras, aunque también pueden influir factores ecológicos y biológicos no térmicos en la diversidad fenotípica a diferentes altitudes.

Palabras clave: Regla de Bergmann, Regla de Allen, variación fenotípica, gradiente altitudinal, aves andinas.

INTRODUCTION

Geographic variation within a species may reflect genetic differentiation among populations, as well as phenotypic responses to local environments (Mayr, 1963; Zink and Remsen, 1986). In this context, phenotypic variation arises from underlying genetic factors, which are shaped by either adaptive or neutral processes (Cadena et al., 2011; Lee et al., 2016), as a consequence of environmental influences and spatial isolation (Amézquita et al., 2009, Goldenberg et al., 2022; Paulo et al., 2003). Among phenotypic traits, morphological characteristics have been widely studied given their ecological and evolutionary importance (Bolívar-Leguizamón & Silveira, 2015; Moreno, 2017; Servino et al., 2024).

Morphological traits influence a variety of ecological and life-history processes (Blackburn and Gaston, 2001; Moreno, 2017). Understanding morphological variation can inform assessments of individual body condition (Moreno, 2017) and reveal the outcomes of geographic isolation or local adaptation (Lee et al., 2021; Busi et al., 2020). Consistent patterns of body size variation along environmental gradients have been described through a set of ecogeographic rules (Lee et al., 2021; Goldenberg et al., 2022), which provide a framework for interpreting shape and size variation across climates and regions (Delhey, 2019). Among these, Bergmann's and Allen's rules are the most well-studied. According to Bergmann's rule, individuals tend to be larger in colder environments and smaller in warmer ones (Bergmann, 1847; Busi et al., 2020). In contrast, Allen's rule states that endotherms have shorter appendages (e.g. limbs, tails and bills) in cold climates, and longer appendages in warm ones (Allen, 1877).

Essentially, they posit a correlation between body size and appendage dimensions and ambient temperature (often via latitude or elevation), grounded in the principles of energy conservation and thermoregulation (Meiri, 2011; Freeman, 2016). Under Bergmann's rule, larger bodies have a lower surface-area-to-volume ratio and thus lose heat more slowly, retaining warmth more effectively (Cardilini et al., 2016; Romano et al., 2019). Under Allen's rule, shorter appendages reduce relative surface area and minimize heat loss, whereas longer appendages increase surface area and facilitate the dissipation of excess heat (Miller et al., 2018; Busi et al., 2020).

Ecogeographical rules have been tested across a wide range of taxa and at multiple levels (intraspecific, interspecific and community) along both latitude and elevation gradients (Ashton, 2002; Maestri et al., 2016; Dangol et al., 2022; Andrade-González et al., 2023). However, results have been mixed. A recent large-scale study revealed that numerous terrestrial vertebrates adhere to Bergmann's rule (Guo et al., 2024), suggesting that larger body size in colder regions may evolve through local adaptation.

In contrast, evidence for Allen's rule is inconsistent; variation in appendage size may be driven by selective pressures such as diet, locomotion or flight requirements, which can override thermal considerations (Friedman et al., 2019; Xu et al., 2023). These discrepancies may arise, at least in part, from the traditional approach of evaluating Bergmann's and Allen's rules independently. Recently, Baldwin et al. (2023) proposed an integrative framework in which both rules operate in a complementary manner. In birds, they showed that subtle and coordinated changes in body size and appendage dimensions can maintain a relatively stable surface-area-to-volume ratio, which represents the true adaptive target of morphological responses to thermal gradients.

The Andean region, with its steep elevation gradients and myriad ecosystems, harbor an extraordinary diversity of birds (Herzog et al., 2011). These sharp environmental gradients provide a natural laboratory in which to study adaptive variation (Fjeldså et al., 2012; Poblete et al., 2023). However, surprisingly few studies have examined how avian morphology varies with elevation in this region (Seeholzer and Brumfield, 2017; Busi et al., 2020). This is a notable gap given that morphological analyses along environmental gradients can provide valuable insights into ecological and evolutionary processes (Ibarguchi, 2011; Díaz et al., 2023).

Relatively few oscine passerine lineages have adapted successfully to the hypoxic, cold conditions of the high Andes (Martin et al., 2023). Among these lineages is the Passerellidae family. The Rufous-collared Sparrow (*Zonotrichia capensis*), a passerellid, is a widespread species that exhibits significant morphological, physiological, behavioural, migratory and vocal variation across its range (Bulau et al., 2018; Poblete et al., 2023). This species' distribution extends from Mexico to southern Argentina (Chapman, 1940), spanning almost the entire South American continent (Cheviron et al., 2008; Danner et al., 2017). In Peru, it occurs from sea level up to about 4600 m, occupying diverse habitats ranging from coastal deserts to the high Andean puna and Amazon region (Schulenberg et al., 2010; Loughheed et al., 2013; Ugarte & Lavalle, 2018).

Despite its wide distribution in Peru, studies evaluating morphological variation in the Rufous-collared Sparrow remain scarce, and even fewer have tested ecogeographical rules in this species. For instance, Castro et al. (1985) found no difference in oxygen consumption between sparrow populations at sea level and at an elevation of around 4,500 m, suggesting some degree of physiological consistency across elevations. Similarly, an assessment of museum specimens in southern Peru reported no significant morphological differences between the sexes (Llerena, 2018), and Davis and Burt. (2019) evaluated Bergmann's and Allen's rule in *Z. capensis* in central Peru, documenting a pattern consistent with Bergmann's rule but finding no clear evidence supporting Allen's rule.

However, extrapolating these results to the southern Andes is limited by pronounced environmental differences among regions. The Arequipa region (see Study Area) is characterized by rugged topography and steep elevational gradients; moreover, the interaction between the Andean Cordillera and the coastal influence of the Pacific Ocean generates strong climatic contrasts (Marengo et al., 2008; Zeballos, 2020). Regional climatic studies have further documented an inverse relationship between elevation and temperature (Moraes et al., 2021), resulting in high thermal heterogeneity across relatively short spatial scales. Recent approaches, particularly in birds, suggest that Bergmann's and Allen's rules operate in a complementary rather than independent manner, maintaining a relatively stable surface-area-to-volume ratio under varying thermal conditions (Baldwin et al., 2023).

In this context, evaluating both rules in *Z. capensis* populations from the Arequipa region not only expands our understanding of ecogeographical patterns in this species, but also provides an opportunity to test the complementary framework for interpreting morphological variation along elevational gradients.

MATERIALS AND METHODS

Study Area

The study was conducted in the Arequipa region of southwestern Peru, on the Pacific slope of the Andes. The region is located between 14°36'06" and 17°16'54" S latitude, and between 70°50'24" and 75°05'52" W longitude, with elevations ranging from 0 to 6,425 m a.s.l. (Marengo et al., 2008; Zeballos, 2020). Due to the presence of the Western Andes Cordillera, the region exhibits a rugged coastal and highland topography, extending from a narrow coastal desert through lomas, pampas, and valleys to an Andean altiplano characterized by very steep and abrupt slopes (Marengo et al., 2008). In addition, the Andes have generated a wide variety of climatic conditions along the altitudinal gradient, ranging from arid and temperate climates along the coast, through semi-arid inter-Andean valleys, to cold and humid climates at higher elevations (Jiménez et al., 2006; Bedoya-Cuno et al., 2024; Castro et al., 2021). The region also includes nine hydrographic basins that drain into the Pacific Ocean (Zeballos, 2020). For this study, sampling transects were established along two of the main basins: the Camaná–Majes–Colca (CMC) basin and the Quilca–Vitor–Chili (QVC) basin, which encompass a broad altitudinal gradient and include different ecosystems with distinct plant and animal communities (Zeballos, 2020).

Table 1. Sampling localities evaluated in the region of Arequipa. The asterisk indicates localities that were captured in the field. CMC = Camaná-Majes-Colca basin, QVC= Quilca-Vitor-Chili Basin.

Tabla 1. Localidades de muestreo evaluadas en la región de Arequipa. El asterisco indica las localidades que fueron capturadas en campo. CMC = Cuenca Camaná-Majes-Colca, QVC = Cuenca Quilca-Vítor-Chili.

Basin	Locality	Longitude	Latitude	Elevation (m a.s.l.)
CMC	Pucchún*	-72.77426	-16.60337	6
	Camaná	-72.64728	-16.51686	100
	Aplao*	-72.48607	-16.07022	618
	Coporaque*	-71.64651	-15.63184	3561
	Chivay	-71.60841	-15.64161	3650
	Canocota	-71.56562	-15.56161	3683
QVC	Quilca*	-72.4209	-16.71746	8
	Vítor*	-71.92272	-16.46516	1166
	Arequipa	-71.52275	-16.40014	2386
	Sogay	-71.44046	-16.57026	2570
	Quequeña	-71.44964	-16.55454	2578
	Yura viejo	-71.70753	-16.21765	2618
	Chiguata*	-71.40166	-16.40417	2900
	Polobaya chico	-71.36878	-16.56432	3048
	Mosopuquio	-71.35369	-16.4517	3297
	San Juan Tarucani	-71.3204	-16.37777	3800

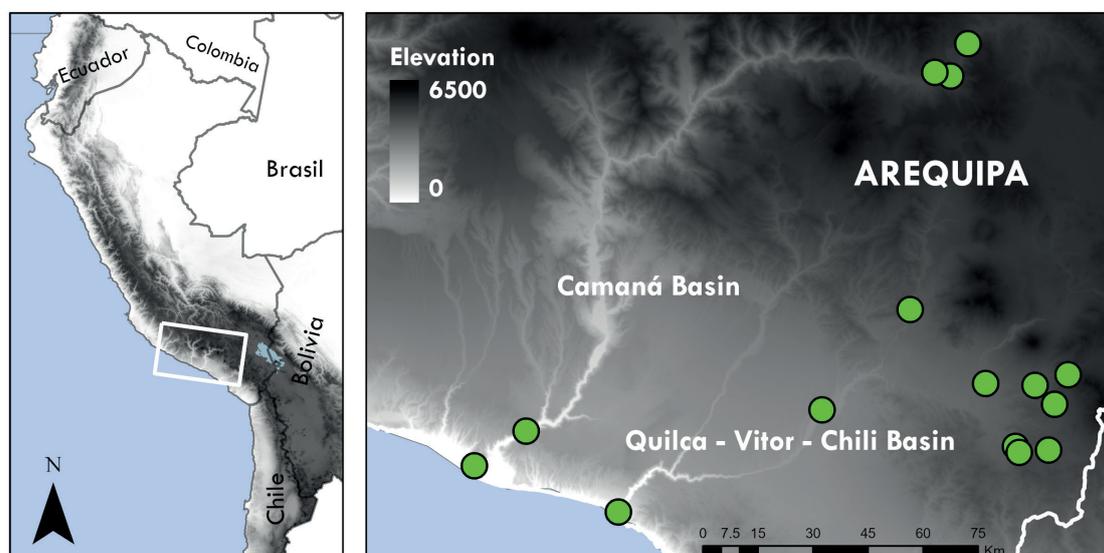


Figure 1. Map showing the evaluated sampling localities in the Arequipa region, Peru (green circles).

Figura 1. Mapa que muestra las localidades de muestreo evaluadas en la región de Arequipa, Perú (círculos verdes).

Taking into account environmental diversity and accessibility, we selected six local field sites (three per basin, Table 1) for live sampling. These sites cover an elevational range from ~6 m (coastal desert) to ~3,800 m above sea level (upper Andean zone). To extend our coverage of the altitudinal gradient (up to ~3,800 m) and increase the size of our sample, we also included data from ten additional localities (Table 1), obtained from specimens housed at the Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA) in Arequipa (see Figure 1). All of the selected localities are within the Arequipa region.

Morphometric Data

Following Cardilini et al. (2016) and Busi et al. (2020), we measured seven morphological traits. Body mass, an index of overall body size pertinent to Bergmann's rule, was measured to the nearest 0.1 g using a digital scale (López et al., 2015). To assess Allen's rule, we measured six appendage traits: wing length (unflattened wing chord from the carpal joint to the tip of the longest primary feather), tail length (length of the rectrices), tarsus length (from the ankle joint to the distal end of the tarsometatarsus), bill length (exposed culmen from the base of the bill to the tip), bill width at the nares and bill depth (height) at the nares. All measurements were taken by the same person with a digital caliper with a precision of ± 0.1 mm or a metal ruler with a precision of ± 0.5 mm was used for linear dimensions and a digital scale was used for mass. The exact same measurement protocol was applied to both live birds and museum specimens to enable comparison.

Morphometric data were obtained from field-collected individuals and preserved museum specimens of *Z. capensis*. Rufous-collared sparrows were captured using mist nets at six field sites between March and June 2023, a period coinciding with the species' breeding season (Díaz et al., 2023). At each site, five mist nets (12 m long \times 3 m high, with 36 mm mesh; Ralph et al., 1996) were operated during the morning (07:00–10:00 h) and in the afternoon (14:00–17:00 h). All captured birds were handled, measured and released on site after processing. Since morphometric traits can vary with age, only adult individuals were selected. As this species lacks external sexual dimorphism, the sex of live birds was determined by the presence of reproductive characteristics: females were identified by a brood patch, while males were identified by the presence of a cloacal protuberance in reproductively active individuals (Pyle, 1997; Cardona-Salazar et al., 2021; Zamorano, 2023). Individuals without clear sex-specific traits (brood patch and cloacal protuberance) were recorded as 'sex undetermined' to avoid misclassification. For museum specimens, we recorded sex, original body mass and locality information from specimen labels.

We then measured six linear morphometric traits on each specimen, using the same protocol as for live birds (we did not measure body mass for preserved skins, relying instead on the field mass recorded on labels). All necessary permits for bird capture and handling were obtained from the Peruvian wildlife authority (Administrative Resolution N° D000315-2022-MIDAGRI-SERFOR-ATFFS-AREQUIPA and N° D000016-2023-MIDAGRI-SERFOR-ATFFS-AREQUIPA).

Statistical Analyses

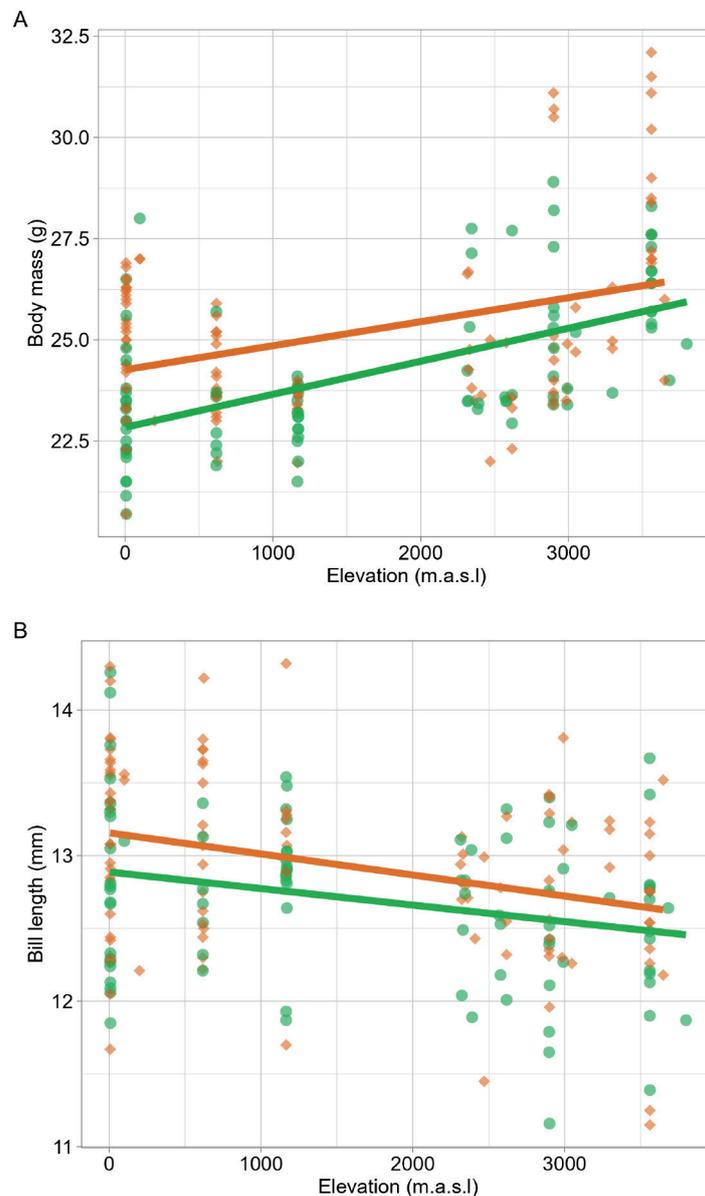
Prior to modelling, we assessed multicollinearity among the seven morphometric variables by calculating all pairwise Pearson correlation coefficient for each pair of variables. As no trait pairs were strongly correlated (all $|r| < 0.6$), all variables were retained for subsequent analyses (Dangol et al., 2022). The morphometric measurements were analyzed in absolute terms in order to directly evaluate phenotypic variation associated with the elevational gradient. We then fitted generalized linear mixed models (GLMMs) with Gaussian errors to evaluate the effects of elevation, sex, and river basin on each morphometric trait. Separate GLMMs were fitted for each response variable (i.e. each morphometric measurement analyzed in turn). Fixed effects included elevation (continuous and scaled), sex (male/female), and river basin (CMC vs. QVC), while locality was specified as a random intercept to account for non-independence at the site level. To facilitate interpretation, elevation was recorded in meters but slopes are reported per 1,000 m (1 km). In exploratory fits, interaction terms (sex \times elevation, basin \times elevation) were evaluated and were retained only if they improved the model fit. In the final models neither interaction term was supported, so both were omitted for parsimony. Model assumptions were checked by visually inspecting of residuals (Q–Q plots and residuals versus fitted plots) and by verifying homoscedasticity; no substantial deviations were detected. To infer fixed effects, P-values were obtained via likelihood-ratio tests comparing full and reduced models (type II), and uncertainty was summarized with 95% confidence intervals around estimated coefficients. GLMMs were fitted using the lme4 package (Bates et al., 2015) in R version 4.3.1 (R Core Team, 2024).

RESULTS

We analyzed a total of 192 Rufous-collared Sparrows, from 16 localities in the Arequipa region, spanning elevations from 6 to 3,800 m above sea level (103 males, 89 females). Of these, 150 individuals (80 males, 70 females) were captured in the field, while the remaining 42 (23 males, 19 females) were museum specimens for which complete data on location, sex, and body mass were available.

No significant trends were found between any of the morphometric traits and the two study basins (CMC and QVC; all $P > 0.05$), and individual variability exceeded variation among localities. In accordance with Bergmann's rule, body mass increased significantly with elevation (slope = 0.535 g per km, 95% CI = 0.097 to 0.983, $P = 0.032$). On average, males were 0.984 g heavier than females (95% CI = 0.512 to 1.453 g, $P < 0.001$; see Fig. 2A).

Regarding the appendages, bill length decreased significantly with elevation (slope = -0.116 mm per km, 95% CI = -0.206 to -0.027 , $P = 0.022$). Males had significantly longer bill than females (difference = 0.233 mm, 95% CI = 0.069 to 0.399, $P = 0.006$; Fig. 2B). Conversely, wing length increased with elevation (slope = 1.314 mm per km, 95% CI = 0.619 to 2.155, $P = 0.007$; Fig. 2C), but not with the sex ($P = 0.3$).



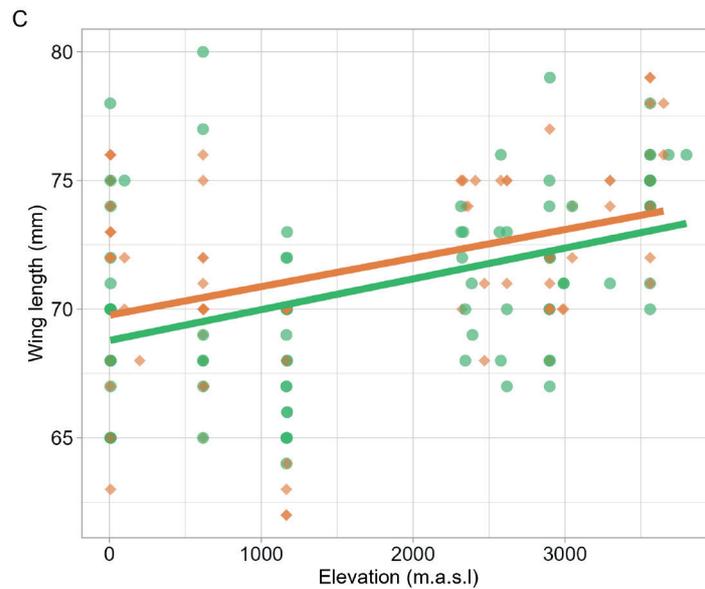


Figure 2. Linear regressions of morphometric measurements of *Zonotrichia capensis*. Orange diamond and line = male, green circle and line = female. A. Body mass vs elevation. B. Bill length vs elevation. C. Wing length vs elevation.

Figura 2. Regresiones lineales de las medidas morfométricas de *Zonotrichia capensis*. Diamante y línea naranja = macho, círculo y línea verde = hembra. A. Masa corporal vs elevación. B. Longitud de pico vs elevación. C. Longitud ala vs elevación.

No significant elevational trends were found for bill height, bill width, tarsus and tail length (all $P > 0.05$). Thus, aside from bill length, none of the measured appendages decreased with altitude; in fact, wing length increased (see Fig. 2C). Consequently, body mass (a proxy for overall body size) increased with elevation as predicted by Bergmann's rule, whereas bill length was the only trait to decrease with elevation, as predicted by Allen's rule, when analyzed independently. Other appendage traits exhibited opposite or no trends with altitude and the sex.

DISCUSSION

Our results support Bergmann's rule, showing an increase in body mass at higher elevations (i.e. in colder conditions). This finding is consistent with patterns observed in many avian taxa globally (Olson et al., 2009; Sun et al., 2017; Guo et al., 2024), and across Neotropical birds (Blackburn and Ruggiero, 2001; Bulgarella et al., 2007; Gutiérrez-Pinto et al., 2014). This corroboration of Bergmann's rule is consistent with the expectation of a thermoregulatory advantage in cold environments, whereby larger individuals have a lower surface-to-volume ratio, thereby reducing heat loss and energy expenditure (Bergmann, 1847; Bulgarella et al., 2007; Martín et al., 2023).

Nevertheless, Bergmann's rule should not be generalized as a universal pattern, as variation in body size may differ among taxa, traits, measurement approaches, and ecological, physiological and evolutionary pressures (Watt et al., 2010; Meiri, 2011). For instance, while our findings (which use body mass as a proxy for body size) differ from those of Busi et al. (2020), who did not observe a clear increase in body size with altitude, they concur with those of Davis and Burt (2019), who used tarsus length as an indicator of body size. Alternative strategies may include increasing plumage insulation or fat reserves, adjust physiological traits (e.g. reduced conductance) and make other structural and behavioral adaptations to cope with colder climates (Gutiérrez-Pinto et al., 2014; Boyle et al., 2016; Fan et al., 2019; Martín et al., 2023).

Furthermore, factors beyond temperature, such as humidity, seasonality, geographic context and resource availability, likely influence the variation in body size observed (Meiri et al., 2007; Diaz et al., 2023).

Contrary to our initial expectations based on Allen's rule, only bill length decreased with increasing elevation among the appendages measured. Allen's rule posits that bill size is subject to thermoregulatory selection; indeed, bird bills are highly vascularized organs capable of significant heat exchange through the rhamphotheca (Tattersall et al., 2009; Greenberg et al., 2012). Our finding of smaller bills in colder, high-altitude environments is consistent with this theory, as has been reported in various bird species (Cardilini et al., 2016; Dangol et al., 2022; Romano et al., 2019). However, exceptions have been documented; in some cases, bill length increases with altitude (Ballentine et al., 2013), and Busi et al. (2020) found no altitudinal differences in the bills of *Z. capensis*. Since the avian bill serves multiple functions beyond heat dissipation, its morphology is influenced by a variety of selective pressures. These include factors such as habitat and feeding ecology (Ballentine et al., 2013; Cardilini et al., 2016), nest building, preening and vocalization (Podos, 2001; Lee et al., 2021). These diverse pressures mean that, even within a single species, populations may exhibit different bill shapes independently of simple thermal gradients (Romano et al., 2019).

By contrast, wing length did not conform to Allen's rule in our study: this trait increased with elevation instead of decreasing. Some studies use wing length as a proxy for overall body size in the context of Bergmann's rule (Meiri and Dayan, 2003; Gutiérrez-Pinto et al., 2014). Here, however, we considered it as appendage within Allen's framework. The increase in wing length at higher elevations is consistent with findings in other bird species (see Sun et al., 2017; Dangol et al., 2022). and is likely to reflect aerodynamic advantages in thin, high-altitude air. At higher elevations, where air pressure is lower and winds are stronger, longer wings can enhance flight efficiency, maneuverability and stability (Bears et al., 2008; Busi et al., 2020) and may facilitate better dispersal in montane environments (Ocampo-Peñuela, 2024).

Factors such as foraging mode, locomotion and flight requirements, diet or habitat structure (VanderWerf, 2012; Gutiérrez-Pinto et al., 2014; Xu et al., 2023), as well as species-specific evolutionary histories (Symonds and Tattersall, 2010; Xu et al., 2023) can influence wing morphology.

However, recent studies suggest that evaluating Allen's rule independently may underestimate its adaptive relevance. Baldwin et al. (2023) demonstrated that, in birds, Bergmann's and Allen's rules often operate in a complementary manner, such that subtle and coordinated changes in body size and appendage dimensions allow adjustment of the surface-to-volume ratio without requiring pronounced variation in a single trait. Under this integrative framework, the detection of weak or inconsistent patterns in individual appendages—such as wings—does not necessarily represent a true deviation from Allen's rule; rather, increased wing length may contribute indirectly to the organism's overall thermodynamic balance, even when this trait is primarily shaped by functional pressures related to flight.

We also observed clear sexual dimorphism, with males being heavier and having longer bills than females. This contradicts earlier reports. For example, Castro et al. (1985) found no significant sex-based differences in oxygen consumption or body metrics when examining *Z. capensis* from sea level to 4500 m. Similarly, Llerena (2018) reported no morphometric dimorphism between male and female specimens in southern Peru. This result may be due to our use of a larger sample size than previous studies and our focus on the breeding season (particularly for field specimens), so the larger size in males could reflect the influence of sexual selection (Lee et al., 2021). In many bird species, larger males have a competitive advantage in territorial disputes, courtship and defense of resources (Searcy, 1979), and it is likely that the ecology of our sparrow follows this pattern (Bears et al., 2008; Busi et al., 2020). Furthermore, there is a link between bill size and song production: males with larger bills may produce more effective songs or calls to attract mates (Chapman, 1940; Danner et al., 2017), which provides a potential reproductive benefit that could drive the evolution of larger bills in males.

In summary, our findings show that, along the altitudinal gradient in Arequipa, *Z. capensis* conforms partially to Allen's rule, but fully to Bergmann's rule. These sparrow populations appear to be adapted to their specific local environmental conditions (Busi et al., 2020). Furthermore, aside from thermoregulatory constraints, it is likely that other ecological and biological factors play a significant role in shaping the observed phenotypic plasticity, potentially limiting or promoting variation in body size and appendage dimensions (Fröhlich et al., 2023). However, these patterns should not be interpreted as isolated confirmations or refutations of classical rules, but rather as expressions of a complex adaptive process in which multiple traits jointly contribute to maintaining a functional thermoregulatory strategy under specific ecological constraints (Baldwin et al., 2023; Fröhlich et al., 2023).

Finally, it is important to acknowledge the limitations of our study. For instance, our sampling was confined to one region of southern Peru, and we used elevation as a proxy for temperature without taking direct climate measurements. These factors should be considered when generalizing the results. Future studies incorporating climatic data and covering broader geographic ranges would help determine how universally these ecogeographic patterns apply to *Z. capensis*. Despite these limitations, our study sheds new light on how Andean bird populations adopt different strategies to adapt to a rapidly changing environment.

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AUTHOR CONTRIBUTIONS

MSH carried out the methodology, investigation, data curation, software, and writing (original draft preparation); VGT and DEV were responsible for conceptualization and writing (review and editing).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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