# DOWN FEATHER STRUCTURE VARIES BETWEEN HIGH AND LOW ELEVATION MALE ANDEAN TORRENT DUCKS (*MERGANETTA* ARMATA)

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**Abstract**

Feathers are one of the defining characteristics of birds and serve a critical role in thermal insulation and physical protection against the environment. Feather structure is known to vary among individuals, and it has been suggested that populations exposed to different environmental conditions may exhibit different patterns in feather structure. We examined both down and contour feathers from two populations of male Torrent Ducks (*Merganetta armata*) from Lima, Peru, one highland population from the Chancay-Huaral River at approximately 3500 meters above sea level (m.a.s.l.) and one lowland population from the Chillón River at approximately 1500 m.a.s.l.. Down feather structure differed significantly between the two populations. Ducks from the highland population had longer, denser down compared with lowland individuals. Contour feather structure varied greatly between individuals but showed no significant difference between populations. These results suggest that the innermost, insulative layer of plumage (the down), may respond to lower ambient temperatures in higher elevations. The lack of observable differences in the contour feathers may be due to the general constraints of the waterproof capability of this outer plumage layer.

**Key Words: contour feather, down feather, feather structure, Merganetta armata, Peru temperature variation**

**Resumen**

El plumaje es una característica que define a las aves y cumple roles críticos en el aislamiento térmico y protección física del ambiente. Se sabe que la estructura de las plumas varía ente individuos, y se ha sugerido que poblaciones expuestas a diferentes condiciones ambientales pueden exhibir diferentes patrones en la estructura de las plumas. En este estudio se examinaron tanto el plumón como las plumas de contorno de machos adultos del Pato de los Torrentes (*Merganetta armata*) de dos poblaciones, una en el río Chancay-Huaral a 3,500 msnm y otra en el río Chillón a 1,500 msnm, ubicadas en Lima, Perú. La estructura de los plumones difiere significativamente entre las dos poblaciones. Los patos de la población a grandes elevaciones tienen plumones largos, y densos comparados con los individuos de las partes bajas. La estructura de las plumas de contorno varía ampliamente entre individuos pero no muestra diferencias significativas entre poblaciones. Estos resultados sugieren que las diferencias entre las capas interiores de aislamiento del plumaje (plumón), pueden ser una respuesta en ambientes de bajas temperaturas a grandes elevaciones. En cambio la falta de detectables diferencias en las plumas de contorno puede ser debido a la constante selección en la capacidad impermeable de la capa de plumas exteriores.

## INTRODUCTION

Plumage is one of the defining characteristics of birds and serves a critical role in multiple functions including communication, flight, and thermal insulation. Indeed, a reigning theory on the original function of primitive feathers is that they enabled early bird-like dinosaurs to evolve homeothermy (Ostrom 1974; Prum and Brush 2002; Pap et al. 2017), and modern plumage acts as a highly efficient thermal buffer against conductive and convective heat loss (Walsberg 1988). All birds shed old and damaged feathers during periodic molts, which is demanding in terms of energy, time, and nutrients so that molting individuals often experience trade-offs between other strenuous periods such as breeding and migration (Murphy & King 1992). Plumage structure varies between species occupying different habitats (Pap et al. 2017), and is also a plastic trait varying between individuals depending on environmental and physiological factors during feather growth (Strochlic & Romero 2008; Butler, Leppert, & Dufty Jr 2010; Moreno-Rueda 2010; Pap et al. 2008, 2013). Therefore, comparing differences in plumage structure in between different environmental conditions can provide insights into the selection pressures that determine this variation.

The body plumage of birds can be broadly divided into two categories: contour, and down. Contour feather structure follows a standard plan of regularly spaced branches (barb) along a central vane (rachis) that has a short basal portion (calamus) imbedded in the skin. Each barb repeats a similar plan with many smaller branches (barbules) densely spaced along either side of the barb. Contour feathers may be further characterized by the exposed, pennaceous (ridged; distal) part of the vane which aids in water repellency and protection, while the plumulaceous (downy; proximal) section provides thermal insulation, and are recognized

through stark differences in barb and barbule texture (Stettenheim 2000; Figure 1). Proportion of plumulaceous barbs, as well as barb and barbule density are thought to determine the amount of air trapped near the skin (Middleton 1986; Butler, Rohwer & Spidel 2008; Broggi et al. 2011, Pap et al. 2017), thereby influencing thermoregulatory capacity (Walsberg 1988). A thicker downy coat composed of longer, denser plumulaceous barbs makes intuitive sense for birds living in colder environments, while birds living in hotter environments should have a looser plumage structure to allow them to prevent heat absorption (Walsberg & King 1978).

In ducks, contour feathers cover most of the body along discrete tracts and provide an impenetrable waterproof covering over a thick layer of insulating down feathers (Stephenson & Andrews 1997; Stettenheim 2000). As the production of feathers is costly, it would be advantageous for individuals to produce an optimal plumage for their given environment. The energetic costs associated with having suboptimal plumage could be substantial in waterfowl, as thermoregulation can account for 28% of the daily energy expenditure (McKinney & McWilliams 2005). Recent years have seen an increase of studies characterizing interpopulation variation of feather structure due to environmental variation (Middleton 1986; Broggi et al 2011; Gamero et al. 2015; Koskenpato et al. 2016), but few have focused on waterfowl or comparative data of down feathers (but see Pap et al. 2017; D'alba et al. 2017).

Torrent Ducks (*Merganetta armata*) are specialized riverine ducks that inhabit many of the rivers along the Andes from Venezuela to Tierra del Fuego (Fjeldså and Krabbe 1990). This species is characterized as a small bodied (350-550g; Alza et al. 2017) diving forager that feeds primarily on aquatic insects by gleaning the surface of submerged boulders (Cerón 2010). *M. armata* form monogamous pairs and both sexes cooperate in the defense an approximate 1-2

kilometer stretch of river where they remain year round (Moffet 1970). *M. armata* is an ideal organism to study the environmental correlates of feather structure as they occur in elevations that range from 300 to over 4,000 meters in elevation (Fjeldså and Krabbe 1990). In Peru, a steep environmental gradient consists of an extremely diverse variety of ecology and topography is present in the west slope of the Andes; with lowland areas along the central coast consisting of hot to mild arid deserts interspersed by lush river valleys and lomas hills that gradually give way to cold semi-arid grasslands and glacial carved montane valleys at higher elevations (Peel, Finlayson & McMahon, 2007; Cheek pers. obs.).

Gutiérrez-Pinto et al. (2014) found a significant difference in morphological traits in male *M. armata* in Peru, with larger males in lowland areas compared to highlands. It was speculated that the physiological strain of living in a hypoxic environment is responsible for the observed difference in body mass and skull length along an elevational gradient, but other physiological mechanisms that could allow *M. armata* to cope in harsh environments (i.e. insulation and daily energy expenditure) have not been fully described. It has been observed that *M. armata* in Peru have very little subcutaneous fat (Gutiérrez-Pinto et al., 2014; Cheek pers. obs.), and a concurrent analysis using the same individuals used in this study found no significant difference in resting $O^2$ consumption between lowland and highland individuals (Ivy pers comm.). Additionally, Dawson et al. (2016) did not find a significant difference in the respiratory capacity in the pectoralis flight muscles of highland and lowland *M. armata* individuals from this study, suggesting these animals do not appear to be altering their metabolic rate to compensate for lower temperatures in higher elevations. Therefore, we predict that *M. armata* plumage

structure will reflect differences due to environmental temperatures associated with high and low elevations.

We compared body plumage by examining down and contour feather structure between two populations of *Merganetta armata* living at two elevational extremes of their distribution further characterized by differences in environmental temperatures. This allowed us to address the question: Do key feather structure attributes in *M. armata* insulation change between populations living in different elevations and temperatures?

## METHODS

Twelve adult, male *Merganetta armata* were collected from two rivers in the Lima region of Peru (Appendix); six individuals in the Rio Chancay-Huaral (>3,000 m.a.s.l., Figure 2), and six individuals in the Rio Chillón (<2,000 m.a.s.l., Figure 2), hereafter referred to as the highland and lowland population respectively. The highland study area consists of alpine river valleys with mean annual temperatures of approximately 12ºC and water temperatures of 11ºC (Vargas, Ministerio de Agricultura y Riego 2015). The lowland study area consists of a mosaic of farmland and thick vegetation along the riverbank, characterized by mean annual temperatures of approximately 20ºC and water temperatures of 19ºC (Ayala, Ministerio de Agricultura y Riego 2013). Though the two populations are geographically isolated, there is moderate levels of gene flow between and across the river systems (Alza et al. unpublished data), indicating that the populations are not genetically structured.

Ducks from the highland and lowland populations were euthanized from 7$^{th}$ to 18$^{th}$ August 2015 as part of a concurrent study by the University of Miami and McMaster University

(Dawson et al. 2016). There is no reason to expect differences in timing of molt to be a factor, as all animals were sampled within the same two-week time span. Skins were collected from each animal, coated in salt, and stored in a -18ºC freezer until subsequent analysis. Feather structure analyses were undertaken in January 2016 in the Centro de Ornitología y Biodiversidad (CORBIDI) satellite laboratory in Lima, Peru. After the skins were thoroughly washed and dried, five down and five contour feathers (minimal size for a boxplot comparison, Krzywinski & Altman 2014) were randomly plucked from the upper right pectoral tract of each individual. Feathers were plucked and handled with tweezers, and otherwise stored in glassine envelopes. Skins were later deposited in the CORBIDI ornithology study skin collection (Appendix).

**Feather Structure**

We measured 6 different traits as described by Middleton (1986) and Broggi (2011) to describe feather structure. Feather length (without calamus) for both down and contour feathers was measured by photographing each feather parallel to a metric ruler. ImageJ software (version 1.50b; Schneider, Rasband, and Eliceiri 2012) was used to calculate length with the measure tool recalibrated for each photo (Figure 1). All photographs and analyses were carried out by the same person (R.C.).

Fine down feather structure was analyzed with the help of a stereoscopic microscope. *M. armata* down plumage is dense, with barbs regularly spaced along two rachides attached to the calamus. To describe down feather structure photographs were taken of a single rachis of each feather at .8X objective with a camera mounted to the lens. Photographs were analyzed using the ImageJ multi-point count tool to determine total number of barbs along a single rachis for each down feather. Additional feather traits were measured for all contour feathers

including: length of plumulaceous portion of each feather, and number of barbs within a 3.5 mm section of the plumulaceous and pennaceous portions of each section (.8X). Thus, the variables measured were the 1) number of barbs, 2) total length of down feathers; density of barbs from the 3) plumulaceous and 4) pennaceous portions of contour feathers, 5) total length of contour feather, and 6) proportion of plumulaceous barbs with respect to all barbs.

**Statistical Analysis**

All data were analyzed in R version 3.3.1 (R Core Team, 2017). All variables except the density of barbs (count data) were normally distributed (Shapiro-Wilk test). To assess the variation in the different feather structure traits by location, we used mixed models controlling for repeated measures (5 feathers per individual). Linear mixed-effects models were used for continuous variables (length and proportion) and generalized linear mixed-effects models for count variables (density of barbs) with a poisson distribution. Each feather trait was a dependent variable, while sampling location (highland and lowland populations, fixed effect), and individual (each of the 12 *M. armata* sampled, random effect) were independent variables. To estimate the confidence intervals for the parameter of the variable, location (fixed effect), we used the R function *confint* for the non-normally distributed count data, and the function *difflsmeans* for the continuous data. Finally, we estimated and compared the coefficient of variation for each feather trait by location.

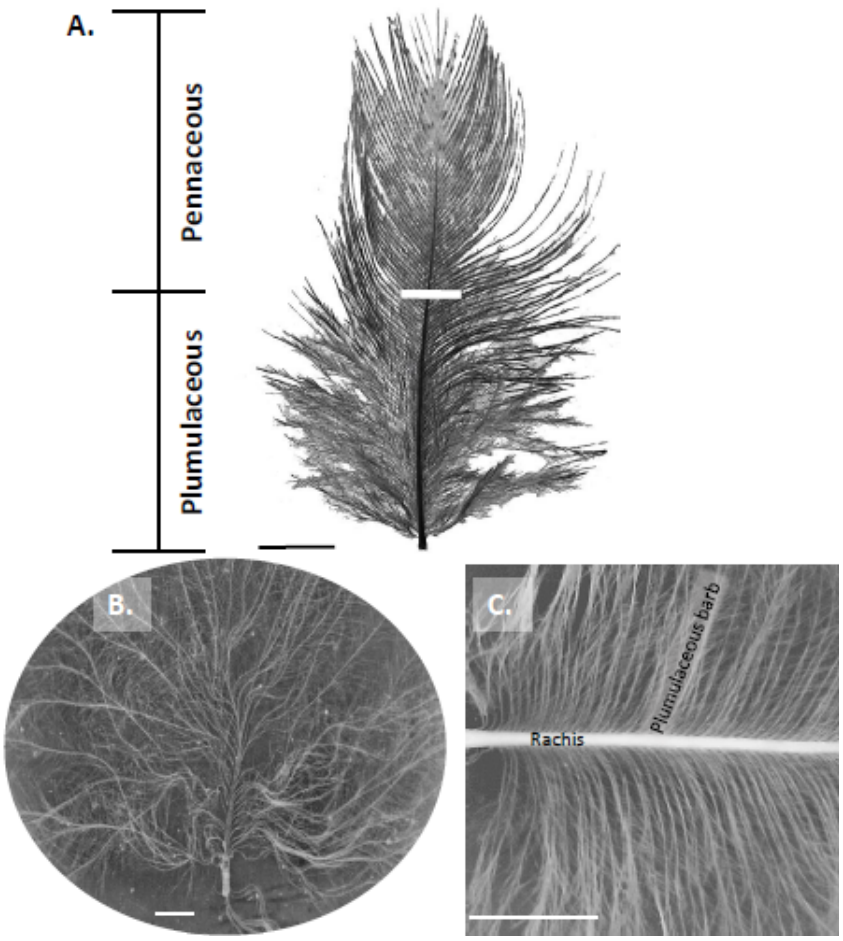


Figure 1. Body feathers of *Merganetta armata* with plumulaceous and pennaceous sections separated by a white stripe across the rachis. The black lines define the boundary of the distal pennaceous and the proximal plumulaceous portions of the feather (A). Lower figures illustrate *M. armata* down (B), and a section of plumulaceous vane with the rachis and barb (C). Scale bars for figure (A) and (C) are 0.5 cm, and (B) is 1 mm.

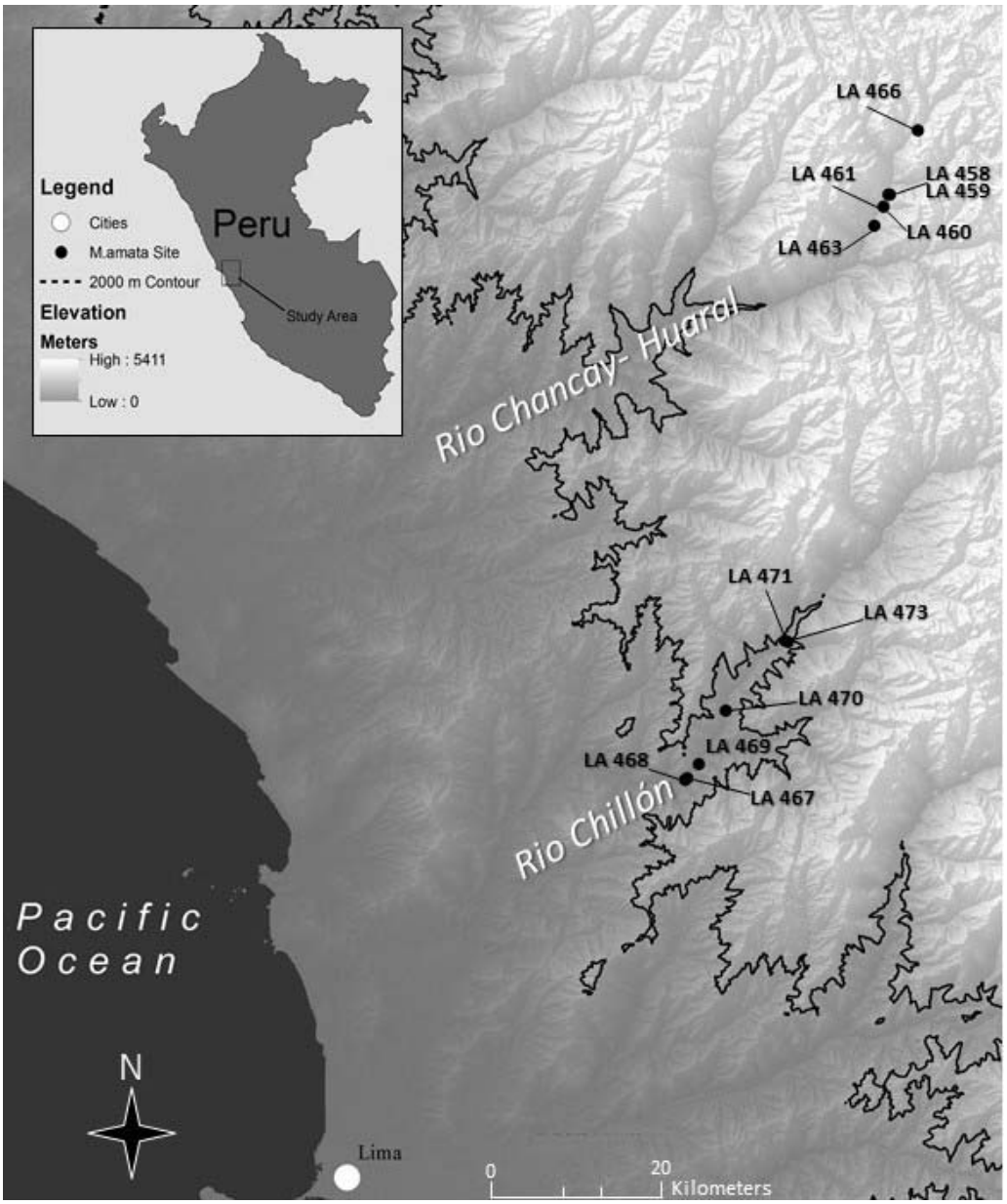


Figure 2. Map of the study area showing the collection sites of the twelve sampled *Merganetta armata* Individuals (Appendix) along the Chillón (lowland population) and Chancay-Huaral (highland population) Rivers in the Lima region of Peru.

RESULTS

Down feathers of highland individuals were, on average, longer and had a greater number of barbs compared to lowland individuals ($F_{Lenth}$=11.815, $P_{Length}$=0.006; $F_{Barbs}$=8.008 $P_{Barbs}$=0.004, df= 10; Figure 3A & 3B). For down length, a 95% confidence interval of the location parameter did not intersect zero $CI_{Length}$ [-3.22, -0.688], and for barb number the parameter did not intersect zero $CI_{Barbs}$ [-0.201, -0.036].

Contour feather structure varied greatly between individuals (length) and showed no significant differences between the two populations. Total length of contour feathers did not differ between the populations ($F_{Length}$=0.099, $P_{Length}$= 0.759, df= 10, $CI_{Length}$ [-2.59,3.45], Figure 3C), and the proportion of plumulaceous barbs relative to total number of barbs showed no significant difference between the two populations ($F_{\pi Plumulaceous}$=1.739, $P_{\pi Plumulaceous}$= 0.216, df= 10, $CI_{\pi Plumulaceous}$ [-0.007, 0.03], Figure 3D). Barb number from the plumulaceous section of the feathers did not differ significantly between the two populations ($F_{BarbsPlumulaceous}$=2.364, $P_{BarbsPlumulaceous}$=0.124, df= 10, Figure 3E) as indicated by a 95% confidence interval using of the location parameter $CI_{BarbsPlumulaceous}$ [-0.143,0.021]. The number of barbs from the pennaceous section was highly variable and the residuals were skewed left by a single noticeable outlier in the lowland population. However, when this outlier was removed there were still no observable differences shown between the populations, so the results presented here include all data ($F_{BarbsPennaceous}$=0.1468, $P_{BarbsPennaceous}$= 0.702, df=10, $CI_{BarbsPennaceous}$ [-0.119,0.080]; Figure 3F).

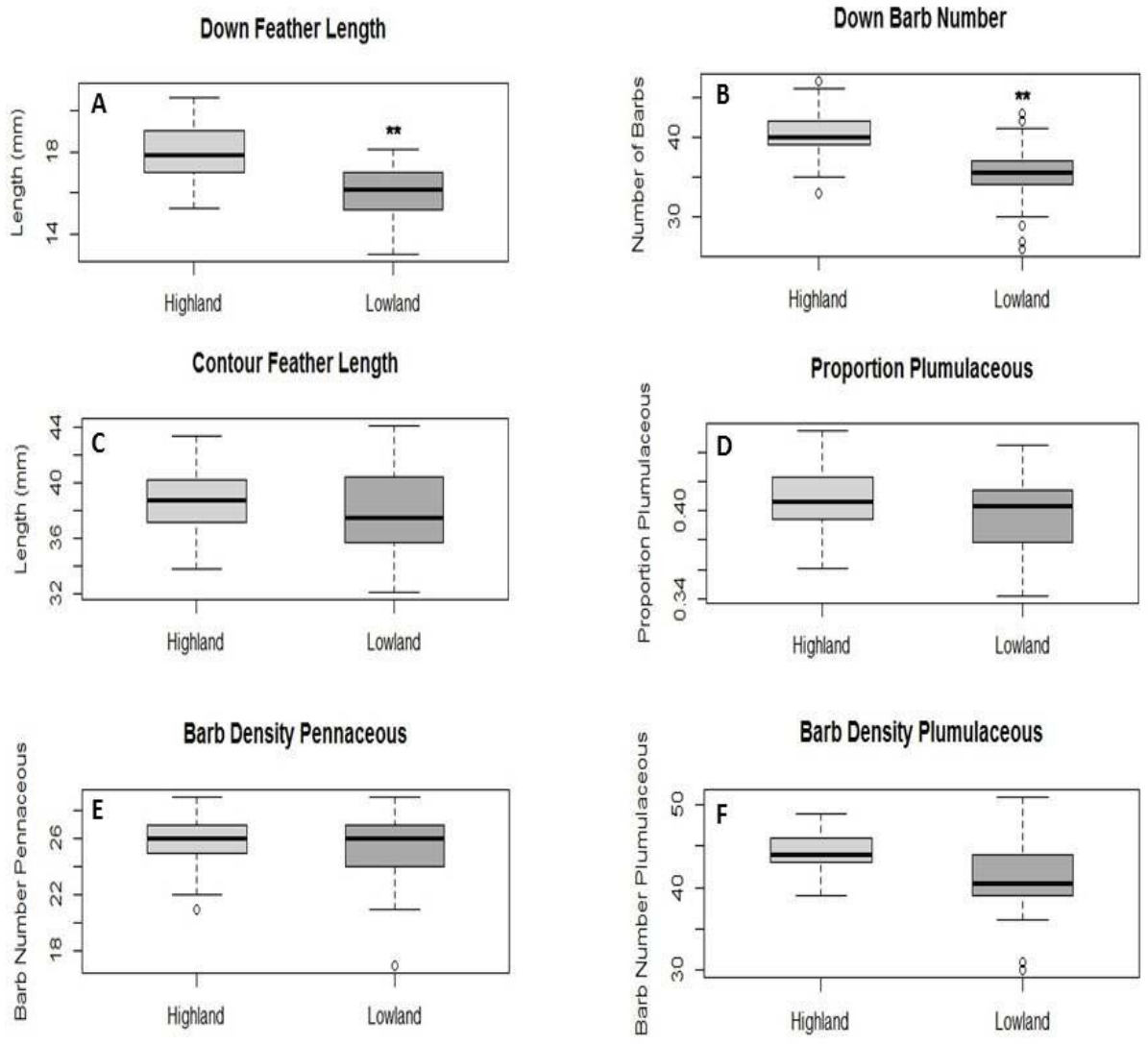


Figure 3. Differences observed in six structural traits of down and contour feathers from the upper right pectoral tracts of twelve adult male *Merganetta armata* from our highland (light grey), and lowland (dark grey) localities in Lima, Peru. Asterisks (*) indicate significant differences between the two populations. Levels of significance: *$P < 0.05$; **$P < 0.01$.

Table 1. Coefficient of variation (CV) of feather structure trait averaged between lowland and highland populations of adult male *Merganetta armata* from Lima, Peru.

| | **Down Length (mm)** | **Down Barb Number** | **Contour Total Length (mm)** | **Contour Proportion Plumulaceous** | **Contour Barb Number-Plumulaceous** | **Contour Barb Number - Pennaceous** |
|---|---|---|---|---|---|---|
| **CV Lowland** | **0.0625** | **0.0590** | **0.0713** | 0.0314 | **0.0966** | **0.0613** |
| **CV Highland** | 0.0531 | 0.0286 | 0.0492 | **0.0411** | 0.0369 | 0.0457 |

DISCUSSION

Down structure differed between highland and lowland individuals of adult male *Merganetta armata* in the west slope of the Andes in Lima, Peru. *Merganetta armata* sampled from the highland population study area (Figure 2) had longer, denser down plumage compared to the lowland population (Figure 3). Research has shown that differences in down microstructure are related to differences in insulative properties, as long fibers increase the air-trapping capacity of the feather (D'alba et al. 2017). While our observed differences may appear inconsequential from feather to feather, a difference of 3-4 barbs and 2mm of length in the average down feather across the whole body would have substantial effects on the overall plumage of the animal. This suggests our observed differences in *M. armata* down reflect the demands of contrasting environments in the highlands and lowlands of the Peruvian Andes.

The lack of observable differences between the contour feathers of the highland and lowland populations could be caused by a diversity of constraints compared with down feathers. First, contour feathers were more variable within individuals (five feathers per individual) than between populations (six individuals per population), which could be due to natural variation

among individuals. Second, there is no standard method for quantifying feather structure (Butler et al. 2008), it is possible that different variables in the contour feathers such as: barb angle (Butler, Rohwer, & Speidel 2008), hue values and infrared spectra (Dove et al. 2007; Gamero et al. 2015), or porosity (a function of barb width and spacing) (Rijke 1968, 1970; Rijke & Jesser 2011), are better descriptors of insulation capacity. The methodology applied in this study was adopted because it was cost effective and easily adapted to an unconventional lab space. Other traits worth investigation are barbule density and feather microstructure (D'alba et al. 2017) of *M. armata* down and contour feathers. An attempt was made to measure feather barbule density for this study; however, the power of the microscope used was not sufficient to be able to reliably detect these incredibly minute structures.

Additionally, our findings are consistent with a recent phylogenetic review that found no observable differences in the barb density of plumulaceous and pennaceous sections of contour feathers in aquatic birds across environments (Pap et al. 2017). Since *M. armata* are specialized to a similar habitat type, fast flowing torrential rivers (Johnson 1963), there is no a priori reason to expect contour feathers (i.e. the protective layer of plumage) to differ between highland and lowland populations. In contrast to the contour feathers, the insulative down may be more sensitive to environmental temperatures, particularly in aquatic birds.

Trends in the literature show that analyzing feather structure characteristics is a growing field with a wealth of potential questions that may be answered. Common garden approaches with passerines have shown that birds from higher latitudes with denser insulative plumage expend less energy on thermoregulation than conspecifics from lower latitudes (Broggi et al. 2005, 2011). Comparative studies between species have also shown that feather characteristics

likely reflect the demands of habitat, as aquatic species appear to prioritize waterproofing and plumage cohesion, while terrestrial species show greater variation in insulative properties (Pap et al. 2017; D'alba et al. 2017). Future work should build upon this by investigating patterns of plumage variation among populations between habitats, in addition to further comparison of species across habitats.

The importance of down plumage between species in particular is limited as few studies have focused on environmental correlates influencing down structure (but see Williams, Hagelin, and Kooyman 2015; Pap et al. 2017; D'alba et al. 2017). Our findings represent a novel attempt to quantify interpopulation down feather structure between environments along an elevational gradient. Further investigation of down feather structure, particularly in waterfowl, would help to clarify if the observed pattern of longer, denser down plumage in colder environments is repeated in other species. Studies investigating feather structure of species across elevational gradients to answer whether plumage is determined through evolutionary processes or a plastic response to environmental differences should also be conducted.

We have shown that highland *M. armata* have longer, denser down feathers compared to lowland individuals. Moreover, average plumage traits between localities appeared to vary more in the lowland population compared to the highland individuals sampled (Table 1). This could indicate that *M. armata* plumage is more constrained at higher elevations. Further investigation is needed to determine if this pattern is repeated across drainages. These data suggest that these animals are compensating for colder environments by increasing the insulative capacity of their down plumage thereby potentially avoiding to expend more energy through increased metabolic output for thermogenesis (Dawson et al. 2016; Ivy pers comm).

The lack of observable differences in contour feathers may be related to strong constraints of the waterproof capability of this outer plumage layer. Further investigation is warranted to examine the microstructures of these feathers (D'alba et al. 2017), quantify insulative capacity of the plumage (Walsberg 1988), and determine if these patterns between habitats are repeated across the latitudinal range of *M. armata* subspecies.

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APPENDIX

Adult male specimens used in this study with identifiers (Luis Alza [LA]) catalogue numbers. Collection localities are also included. All voucher specimens are housed in the Centro de Ornitología y Biodiversidad (CORBIDI) ornithology collection, in Lima, Peru.

| **Species** | **Locality** | **Latitude S** | **Longitude W** | **Elevation (meters)** | **Date Collected** | **Catalogue Number** |
|---|---|---|---|---|---|---|
| **Highland** | **Rio-Chancay-Huaral** | | | | | |
| *Merganetta armata* | Vichaycocha | 11.15983 | 76.62881 | 3680 | 7 Aug 2015 | LA 458 |
| *Merganetta armata* | Vichaycocha | 11.15983 | 76.62881 | 3680 | 7 Aug 2015 | LA 459 |
| *Merganetta armata* | Baños de Cóllpa | 11.17059 | 76.63445 | 3193 | 8 Aug 2015 | LA 460 |
| *Merganetta armata* | Vichaycocha | 11.15981 | 76.62981 | 3299 | 8 Aug 2015 | LA 461 |
| *Merganetta armata* | Vichaycocha | 11.18813 | 76.64276 | 3000 | 9 Aug 2015 | LA 463 |
| *Merganetta armata* | Vichaycocha | 11.10174 | 76.60341 | 4086 | 10 Aug 2015 | LA 466 |
| **Lowland** | **Rio Chillón** | | | | | |
| *Merganetta armata* | Santa Rosa de Quives | 11.67533 | 76.80168 | 1092 | 12 Aug 2015 | LA 467 |
| *Merganetta armata* | Santa Rosa de Quives | 11.68945 | 76.81411 | 1034 | 13 Aug 2015 | LA 468 |
| *Merganetta armata* | Santa Rosa de Quives | 11.68801 | 76.81205 | 1040 | 14 Aug 2015 | LA 469 |
| *Merganetta armata* | Fundo Huanchuy | 11.62689 | 76.77708 | 1248 | 15 Aug 2015 | LA 470 |
| *Merganetta armata* | Yaso | 11.56482 | 76.72112 | 1665 | 15 Aug 2015 | LA 471 |
| *Merganetta armata* | Yaso | 11.56362 | 76.72347 | 1615 | 16 Aug 2015 | LA 473 |