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DOWN FEATHER STRUCTURE VARIES BETWEEN LOW- AND HIGH-ALTITUDE TORRENT DUCKS (*MERGANETTA ARMATA*) IN THE ANDES

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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, including one high-altitude population from the Chancay-Huaral River at approximately 3500 m a.s.l. and one low-altitude population from the Chillón River at approximately 1500 m a.s.l.. Down feather structure differed significantly between the two populations. Ducks from the high-altitude population had longer, denser down compared with low-altitude individuals. Contour feather structure varied greatly among individuals but showed no consistent difference between populations. These results suggest that the innermost, insulative layer of plumage (the down), may have developed in response to lower ambient temperatures at high elevations. The lack of observable differences in the contour feathers may be due to the fact that this outer plumage layer is more important as waterproofing than insulation.

Resumen · La estructura del plumón del Pato de los Torrentes (*Merganetta armata*) varia entre bajas y grandes altitudes en los Andes
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 entre 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 3500 m s.n.m. y otra en el río Chillón a 1500 m s.n.m., ubicadas en Lima, Perú. La estructura de plumón difiere significativamente entre las dos poblaciones. Los patos de la población a mayor altitud presentan un plumón más largo, y denso que sus congéneres de menor altitud. 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 haberse desarrollado como respuesta en ambientes de bajas temperaturas a grandes elevaciones. En cambio, la ausencia de diferencias detectables en las plumas de contorno puede deberse al hecho de que esta capa externa es más importante en la impermeabilización que en el aislamiento.

Key words: Andes · Contour feather · Down feather · Feather structure · *Merganetta armata* · Peru · Temperature variation · Torrent Duck

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INTRODUCTION

Plumage is one of the defining characteristics of birds and serves a critical role in multiple functions including communication, flight, and thermal insulation (Stettenheim 2000). 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 & Brush 2002, Pap et al. 2017). Modern plumage acts as a highly efficient thermal buffer against conductive and convective heat loss both in the air and underwater (Walsberg 1988, Novoa et al. 1994). All birds shed old and damaged feathers during periodic molts, which are demanding in terms of energy, time, and nutrients. Plumage structure varies between species occupying different habitats (Pap et al. 2017) and is a highly plastic trait that varies among individuals depending on environmental and physiological factors during feather growth (Strochlic & Romero 2008, Butler et al. 2010, Moreno-Rueda 2010; Pap et al. 2008, 2013). Therefore, comparing the plumage structure between individuals inhabiting different environmental conditions can provide insights into how birds respond to the selection pressures that contribute to 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 (barbs) 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, whereas the plumulaceous (downy; proximal) section provides thermal insulation, recognized through stark differences in barb and barbule texture (Stettenheim 2000; Figure 1). The 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 et al. 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, whereas birds living in hotter environments should have a looser plumage structure to allow them to prevent heat absorption by increasing external surface area of the plumage (Walsberg & King 1978).

In ducks (Anatidae), contour feathers with monoester waxes from the preen gland 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, molting individuals often experience trade-offs during other strenuous periods of the lifecycle such as breeding and migration (Murphy & King 1992, Nilsson & Svensson 1996). It would therefore be advantageous for individuals to produce an optimal plumage for the thermal conditions of their given aquatic or terrestrial 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 in 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, de Zwaan et al. 2016), but few have focused on waterfowl, or on variation of down feathers among species or populations inhabiting different environments (but see Pap et al. 2017, D'alba et al. 2017, Osváth et al. in press).

Torrent Ducks (*Merganetta armata*) are specialized riverine ducks that inhabit many of the rivers along the Andes, from Venezuela to Tierra del Fuego (Fjeldså & Krabbe 1990: 122). This species is characterized as a small bodied (350–550 g; Alza et al. 2017) diving duck that forages primarily on aquatic insects by gleaning the surface of submerged boulders (Cerón 2010). Torrent Ducks form monogamous pairs, and both sexes cooperate in the defense of an approximate 1–2 kilometer stretch of river they inhabit year round (Moffet 1970). The Torrent Duck is an ideal organism to study the environmental correlates of feather structure as they occur in elevations that range from 300 to over 4000 m a.s.l. (Fjeldså & Krabbe 1990: 122). In Peru, a steep environmental gradient usually consists of an extremely diverse variety of ecological and topographic conditions. On the west slope of the Andes, for example, low-altitude areas along the central coast consist of hot to mild arid deserts interspersed by lush river valleys and lomas (hills) that give way to very cold semi-arid grasslands and glacier-carved mountain valleys at higher elevations (Peel et al. 2007, Cheek pers. observ.).

In a recent study of Torrent Ducks across the Andes, Gutiérrez-Pinto et al. (2014) found significant differences in morphological traits associated with elevation in Peru. However, these finding were contrary to what would be expected by Bergmann's rule (Bergmann 1847) regarding temperature, with larger males in warmer, low-altitude areas compared to smaller males in colder, high-altitude areas. This discrepancy in the expected relationship of body size and temperature suggests that other physiological mechanisms (i.e., insulation and daily energy expenditure) may work to allow Torrent Ducks to survive in cold, high-altitude environments.

We compared body plumage by examining down and contour feather structure between two populations of Torrent Ducks living at two elevational extremes of their distribution characterized by strong differences in environmental temperatures. This allowed us to address the question: Do key structural attributes in Torrent Duck feather insulation differ

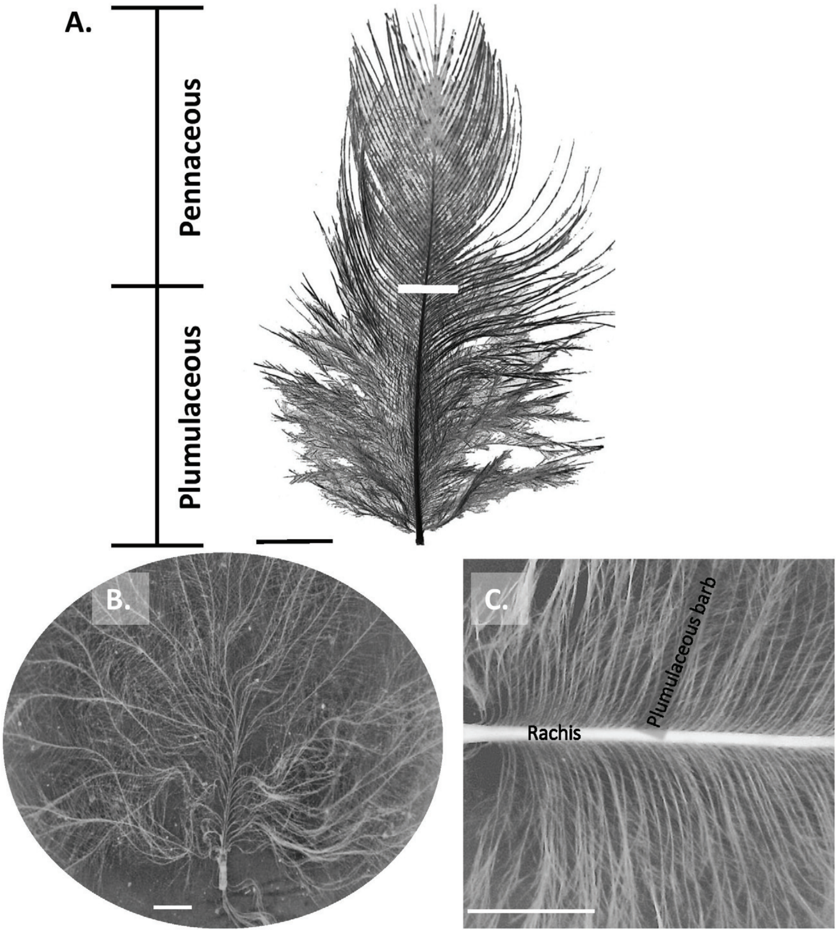

Figure 1. Body feathers of Torrent Ducks (*Merganetta armata*) with plumulaceous and pennaceous sections separated by a white stripe across the rachis. The black lines define the boundary of the distal pennaceous and the proximal plumulaceous portions of the feather (A). Lower figures illustrate Torrent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

between populations living in different elevations and temperatures, and do those differences reflect patterns predicted for a diving duck inhabiting a range of environments?

METHODS

Twelve adult, male Torrent Ducks were collected from two rivers in the Department of Lima, Peru (Appendix); six individuals in the Rio Chancay-Huaral (> 3000 m a.s.l.; Figure 2), and six individuals in the Rio Chillón (< 2000 m a.s.l.; Figure 2), hereafter referred to as the low- and high-altitude populations respectively. The low-altitude study area consists of a mosaic of farmland and thick vegetation along the riverbank, characterized by mean annual temperatures of approximately 20°C and water temperatures of 19°C (Ayala, Ministerio de Agricultura y Riego 2013). The high-altitude study area consists of alpine river valleys with mean annual temperatures of approximately 12°C and water temperatures of 11°C (Vargas, Ministerio de Agricultura y Riego 2015). Though the two populations are distributed in two different but adjacent watersheds with the same water source and Andean orogeny (Figure 2), gene flow levels between and across the populations (i.e., Φ_{ST} between = 0.1, and Φ_{ST} within = 0.05, Control Region mitochondrial DNA) are sufficient to homogenize genotypic and phenotypic differences potentially caused by genetic drift, or natural selection (Alza in prep.). Additionally, preliminary comparisons using the analysis of variance (ANOVA) for morphological characters (mass, culmen length, skull length, and tarsus length) between the two rivers by sex did not show statistically significant differences (Alza in prep.).

Torrent Ducks from the low and high-altitude populations were euthanized from 7–18 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 –18°C freezer until subsequent analysis. Feather structure analyses were undertaken in January 2016 in the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru. After the skins were thoroughly washed and

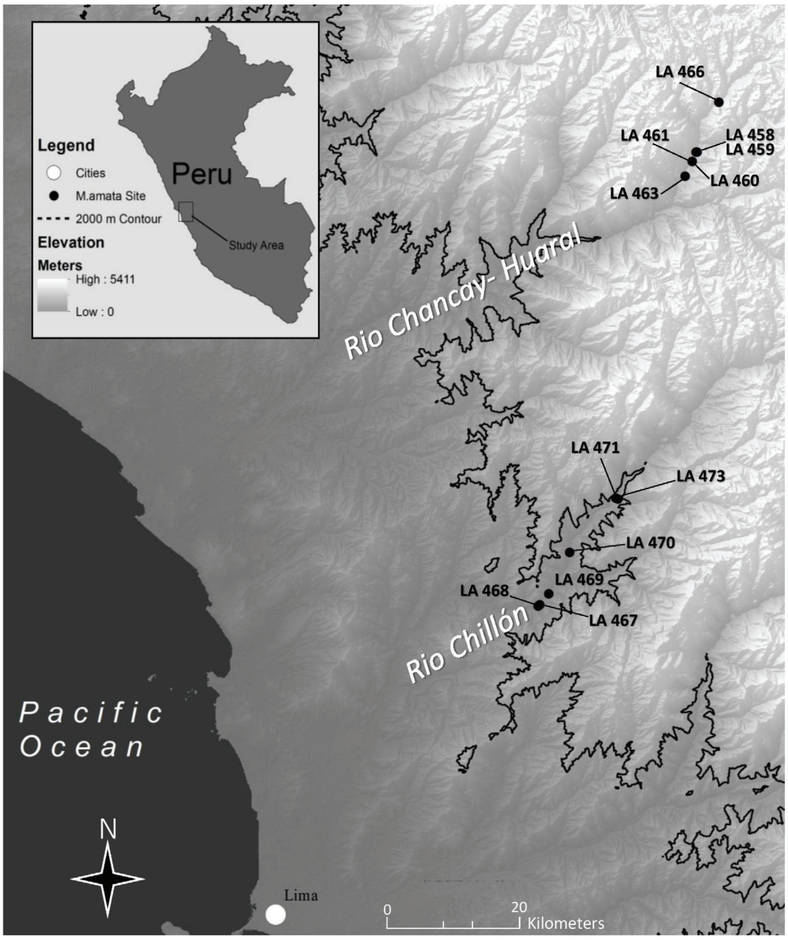

Figure 2. Map of the study areas showing the collection sites of the twelve sampled Torrent Duck (*Merganetta armata*) individuals (Appendix) along the Chillón River (low-altitude population) and Chancay-Huaral River (high-altitude population) in the Department of Lima, Peru.

dried, five down and five contour feathers (minimal sample size for estimate the probability distribution of the data and a boxplot comparison, Krzywinski & Altman 2014) were randomly plucked from the upper right pectoral feather tract of each individual. Feathers were plucked and handled with tweezers, and otherwise stored in glassine envelopes. Skins were later deposited in the Ornithology Study Skin Collection at CORBIDI (Appendix).

Feather structure. We measured six different traits as described by Middleton (1986) and Broggi et al. (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 (mm). ImageJ software (version 1.50b; Schneider et al. 2012) was used to calculate feather length with the measuring tool recalibrated for each photo (Figure 1). All photographs and analyses were carried out by the same person (RC).

Fine down feather structure was analyzed with the help of a stereoscopic microscope. Torrent Duck 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 0.8x 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 (0.8x). 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, 2013). 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 (five 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, whereas sampling location (high- and low-altitude populations, fixed effect), and individual (each of the 12 Torrent Ducks sampled, random effect) were independent variables. Confidence intervals for the location (fixed effect) variable, were calculated using 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.

RESULTS

Down feathers of individual Torrent Ducks from high altitude were, on average, longer and had a greater number of barbs compared to individuals from low altitude (F_{Length} = 11.815, P_{Length} = 0.006; F_{Barbs} = 8.008, P_{Barbs} = 0.004, df = 1, 10; Figure 3A, 3B). For down length and for barb number, the 95% confidence interval of the location parameter did not intersect zero ($\text{CI}_{\text{Length}}$: -3.22, –0.69; CI_{Barbs}: –0.20, –0,04).

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 = 1, 10, $\text{CI}_{\text{Length}}$ [–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 ($F_{\pi\text{Plumulaceous}}$ = 1.739, $P_{\pi\text{Plumulaceous}}$ = 0.216, df = 1, 10, $\text{CI}_{\pi\text{Plumulaceous}}$ [–0.01, 0.03]; Figure 3D). Barb number from the plumulaceous section of the feathers did not differ significantly between the two populations ($F_{\text{BarbsPlumulaceous}}$ = 2.364, $P_{\text{BarbsPlumulaceous}}$ = 0.124, df = 1, 10; Figure 3E) as indicated by a 95% confidence interval of the location parameter $\text{CI}_{\text{BarbsPlumulaceous}}$ [–0.14, 0.02]. The number of barbs from the pennaceous section was highly variable, and the residuals were skewed left by a single noticeable outlier in the low-altitude 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 ($F_{\text{BarbsPennaceous}}$ = 0.147, $P_{\text{BarbsPennaceous}}$ = 0.702, df = 1, 10, $\text{CI}_{\text{BarbsPennaceous}}$ [–0.12, 0.08]; Figure 3F). Average plumage traits between localities varied more in the low-altitude population compared to the high-altitude individuals sampled (Table 1).

DISCUSSION

Down structure differed between low- and high-altitude individuals of adult male *Merganetta armata* in the west slope of the Andes in Lima, Peru. Torrent Ducks sampled from the high-altitude study area (Figure 2) had longer, denser down plumage in the pectoral tract compared to the low-altitude study area (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). This suggests our observed differences in Torrent Duck down reflect the demands of contrasting environments in the low- and high-altitude temperature regimes of the Peruvian Andes.

Metabolic analyses using the same individuals from this study found no significant difference in resting oxygen consumption between low- and high-altitude individuals (Ivy pers. com.). Similarly, Dawson et al. (2016) did not find a significant difference in the respiratory (aerobic) capacity in the pectoralis flight muscles of low- and high-altitude Torrent Ducks. As flight muscles are credited for a majority of thermogenesis in birds (Petit & Vézina 2014), Dawson's results suggest that these animals do not appear to be altering their metabolic rate to tolerate lower temperatures at higher elevations (Marsh & Dawson 1986, Cooper 2002, Broggi et al. 2005, Petit et al. 2017). Therefore, it is possible that high-altitude Torrent Ducks reduce thermogenesis demands by increasing the insulation capacity of their down plumage to reduce heat loss.

The lack of observable differences between the contour feathers of the low- and high-altitude samples could be caused by a diversity of constraints compared with down feathers. First, contour feathers were more variable between individuals (five feathers per individual) than between populations (six individuals per population), which could be due to natural individual variation. Second, there is no standard method for quantifying feather structure (Butler et al. 2008), so it is possible that different variables in the contour feathers such as: barb angle (Butler et al. 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 also good descriptors of insulation capacity. The methodology applied in this study was used because it was cost effective and easily adaptable. Other traits worth investigation are barbule density and feather microstructure (D'alba et al. 2017) of Torrent Duck 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 quantify these incredibly minute structures. Other potential confounding factors not addressed in this study are the effects of variation in total body feather density, waterproofing, and food availability between sampling locations.

It remains to be tested how the whole plumage affects the thermal conductance of Torrent Ducks living in different temperatures. While our observed differences may appear inconsequential from feather to feather, a difference of 3–4 barbs and 2 mm of length in the average down feather across the whole body could be expected to have substantial effects on the overall insulation capacity and rate of heat loss (Walsberg 1988, Wolf & Walsberg 2000). Total body feather density is shown to be strongly associated with envi-

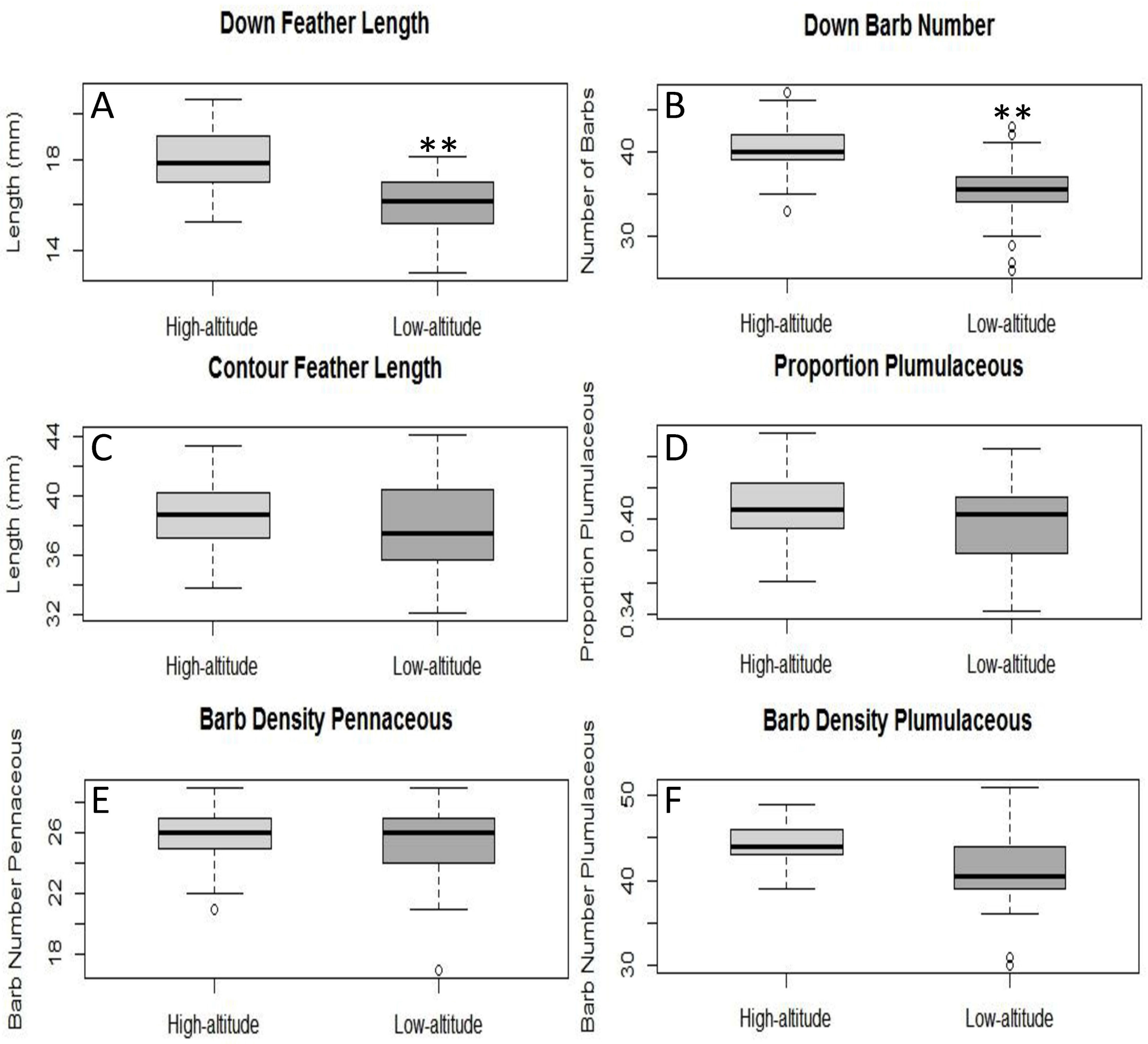

Figure 3. Differences observed in six structural traits of down and contour feathers from the upper right pectoral tracts of twelve adult male Torrent Ducks (*Merganetta armata*) from high-altitude (light grey), and low-altitude (dark grey) localities in Lima, Peru. Asterisks (*) indicate significant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

ronmental conditions (Osváth et al. in press), though primarily across species (but see Middleton 1986, Broggi et al. 2011) and few studies have focused on aquatic birds (Williams et al. 2015). Studies measuring contour and down feather density in waterfowl along elevational gradients are warranted to determine if environmental conditions affect these traits between individuals. Additionally, aquatic birds are further characterized by possessing relatively large uropygial glands, which produce monoester waxes, and oils necessary for waterproofing of feathers during preening (Stettenheim 2000). Further investigation of the functional role these uropygial secretions play across taxa and environmental gradients is warranted to determine the effect waterproofing capabilities have on thermal conductance. Another potentially critical factor we did not address in our study is the variation in food availability between environments. Species abundance of macroinvertebrates is negatively associated with elevation (Lujan et al. 2013), and as food availability directly affects feather structure quality (Pap et al. 2008); high-altitude populations of Torrent Ducks may devote more resources to producing high quality plumage, rather than towards body size (Gutiérrez-Pinto et al. 2014). This could prove to be an informative avenue worth pursuing in future studies.

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 across their range Torrent Ducks 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 low- and high-altitude populations. In contrast to the contour feathers, the insulative down may be more sensitive to environmental temperatures, particularly in aquatic birds. Comparative studies

Table 1. Coefficient of variation (CV) of feather structure traits averaged between low-altitude and high-altitude populations of adult male Torrent Ducks (*Merganetta armata*) from Lima, Peru. Bold numbers indicate higher relative values of CV.

Feather type	Feather trait	CV low altitude	CV high altitude
Down	**Length (mm)**	**0.0625**	0.0531
	Barb number	**0.0590**	0.0286
Contour	**Total length (mm)**	**0.0713**	0.0492
	Proportion-plumulaceous	0.0314	**0.0411**
	Barb number-plumulaceous	**0.0966**	0.0369
	Barb number-pennaceous	**0.0613**	0.0457

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

Our understanding of the importance of down plumage variation between species is limited as few studies have focused on environmental correlates influencing down structure (but see Williams et al. 2015, Pap et al. 2017, D'alba et al. 2017, Osváth et al. in press). Our findings represent a novel attempt to quantify interpopulation down feather structure between environments along an elevational gradient in an aquatic species. Further investigation of down feather structure, particularly in waterfowl, would show whether the observed pattern of longer, denser down plumage of Torrent Ducks in colder environments is repeated in other species. Studies investigating feather structure of species across elevational gradients to discern whether plumage is determined through evolutionary processes or a phenotypic plastic response to environmental differences should also be conducted.

CONCLUSION

We have shown that high-altitude Torrent Ducks have longer, denser down feathers in the pectoral tract compared with low-altitude individuals. Moreover, average plumage traits between localities appeared to vary more in the low-altitude population compared with the high-altitude individuals sampled (Table 1). This could indicate that Torrent Duck plumage is more constrained by selection or developmental plasticity at higher elevations. The data we present here suggest that Torrent Ducks prevent excess energy expenditure in colder temperatures by increasing the insulative capacity of their down plumage thereby decreasing metabolic demand for thermogenesis (Dawson et al. 2016; Ivy pers. comm.). The lack of observable differences in contour feathers may be related to their being less important as insulation and more necessary to maintain the waterproof capability of this important outer plumage layer in a species that forages underwater. 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 Torrent Duck subspecies.

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APPENDIX 1

Adult male Torrent Duck (*Merganetta armata*) specimens used in this study with collector’s identifiers (Luis Alza [LA]) catalogue numbers. Collection localities, coordinates, and elevations (m a.s.l.) are also included. All voucher specimens are housed in the Centro de Ornitología y Biodiversidad (CORBIDI) ornithology collection, Lima, Peru.

River	Locality	Coordinates	Elevation (m)	Date (2015)	Catalogue number
Rio Chancay-Huaral	Vichaycocha	11.15983°S, 76.62881°W	3680	7 Aug	LA 458
	Vichaycocha	11.15983°S, 76.62881°W	3680	7 Aug	LA 459
	Baños de Collpa	11.17059°S, 76.63445°W	3193	8 Aug	LA 460
	Vichaycocha	11.15981°S, 76.62981°W	3299	8 Aug	LA 461
	Vichaycocha	11.18813°S, 76.64276°W	3000	9 Aug	LA 463
	Vichaycocha	11.10174°S, 76.60341°W	4086	10 Aug	LA 466
Rio Chillón	Santa Rosa de Quives	11.67533°S, 76.80168°W	1092	12 Aug	LA 467
	Santa Rosa de Quives	11.68945°S, 76.81411°W	1034	13 Aug	LA 468
	Santa Rosa de Quives	11.68801°S, 76.81205°W	1040	14 Aug	LA 469
	Fundo Huanchuy	11.62689°S, 76.77708°W	1248	15 Aug	LA 470
	Yaso	11.56482°S, 76.72112°W	1665	15 Aug	LA 471
	Yaso	11.56362°S, 76.72347°W	1615	16 Aug	LA 473