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Latitudinal Geographical Variation in Sexual Dimorphism in a Tropical Montane Bird

(Furnariidae: *Pseudocolaptes boissonneautii*)

by

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Undergraduate honors thesis under the direction of

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## Abstract

Geographical variation in sexual size dimorphism and bill dimorphism was investigated in the Streaked Tuftedcheek, *Pseudocolaptes boissonneautii*. Sexual dimorphism, specifically sexual size dimorphism, is common in animals. Sexual size dimorphism (SSD) is often thought to be caused by sexual selection, but may also be due to ecological causes, such as competition for limited resources. In the Streaked Tuftedcheek, sexual dimorphism was found in bill size and shape, as well as wing length. Bill length was more positively correlated with body size in females than in males, but both males and females displayed a negative correlation between bill shape and bill length, namely, the longer the bill was in both sexes, the less curved it tended to be. Sexual size dimorphism and bill dimorphism was investigated in relation to Bergmann's Rule in the Streaked Tuftedcheek, and this tropical montane bird exhibited sexual differences in both traits with respect to latitude. Geographic variation often follows with Bergmann's Rule, which states that body size increases with latitude, but the Streaked Tuftedcheek does not conform to the rule. Body size increased towards the Equator, the opposite of Bergmann's Rule. At the southern end of the distribution ( $\sim 17^{\circ}\text{S}$ ) both sexes were found to have smaller wing lengths and shorter curvier bills than the rest of the range, whereas both sexes were larger near the middle of the range ( $\sim 5^{\circ}\text{S}$ ). Geographical variation in sexual dimorphism was found to be present in both the wing length and especially bill length of *P. boissonneautii*. However, females displayed a greater degree of variation in bill morphology than males geographically. Geographic variation in sexual dimorphism in bill length has not been previously reported in any other species of bird. To understand the causes underlying these patterns, especially this species' unique pattern of geographic differences in bill length dimorphism, further studies are needed on the foraging behavior, breeding habits, and phylogenetics of this species.

## **Introduction**

Sexual dimorphism is a widespread phenomenon in animals, expressed as differences in sexual signals, behavior, morphology, and body size (Kelly 2013, Amadon 1959, Peterson 1996, Berns and Adams 2010). Most species of animals display some degree of sexual dimorphism (Blackburn et al. 1999, Temeles and Kress 2003). Sexual size dimorphism (SSD), the difference in body size between males and females, can arise from sexual selection (Darwin 1874, Andersson 1994), natural selection, or a combination of the two (Darwin 1874, Slatkin 1983). Sexual differences occur in other body parts such as in feeding structures, like the bill in birds, which is not uncommon (Temeles and Kress 2003, Berns and Adams 2010).

Multiple hypotheses have been proposed for the evolution of sexual dimorphism, such as sexual selection or natural selection (Darwin 1874, Slatkin 1984, Shine 1989). Sexual selection usually concerns mate choice by females or male-male competition for access to a mates (Hedrick and Temeles 1989). Sexual selection is often the preferred hypothesis because it can be easily explained (Shine 1989). Alternatively, sexual dimorphism can be caused by natural selection due to ecological differences between the two sexes (Shine 1989, Andersson 1994). In cases of SSD, males and females may differ in the way they use resources, such as diet or reproductive role and investment (Shine 1989, Greenberg et al. 2013), which increases the niche width of the species, therefore reducing competition (Radford and du Plessis 2003). In birds, bill dimorphism is hypothesized to result from pressure to reduce intrasexual competition for food resources (Selander 1966, Temeles et al. 2000, Radford and du Plessis 2004). Sexual differences in feeding ecology exist couple with dimorphism in bill length produces trophic niche segregation (Navarro et al. 2009).

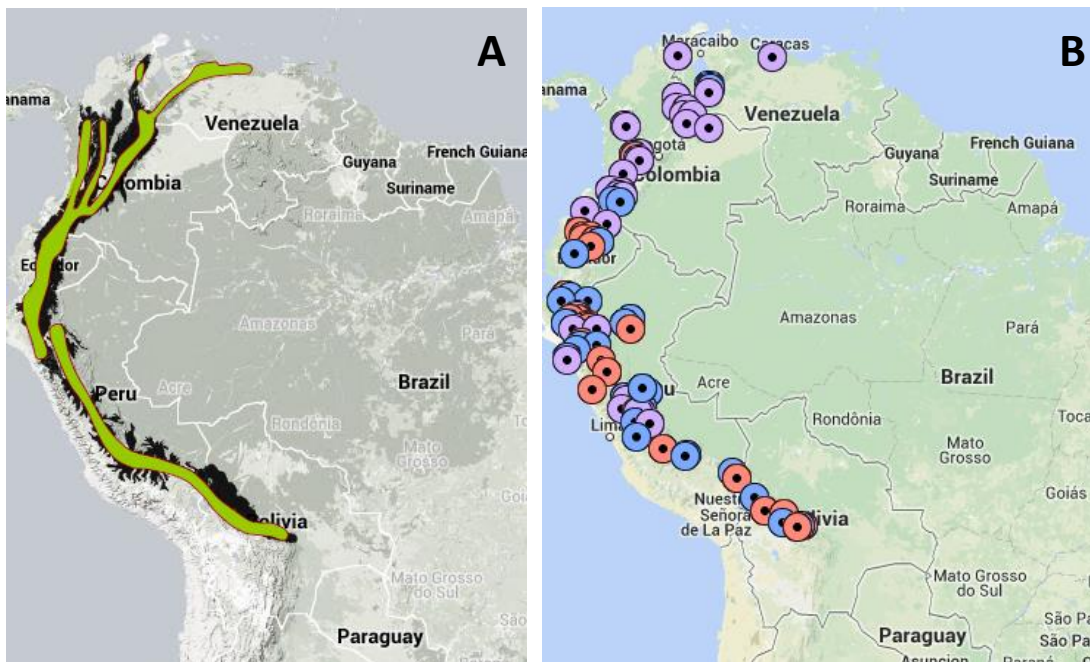
Sexual size dimorphism can vary geographically in some animals such as in birds (Rising 1987) and beetles (Stillwell et al. 2007). This occurs when males and females are more similar in parts of the species' range than in others. Geographic variation could be associated to a latitudinal cline, which is usually studied in the context of Bergmann's Rule (Rensch 1936, Ashton 2002, Stillwell et al. 2007, Berns and Adams 2013), in which body size increases with latitude (Bergman 1847). Because latitude and temperature usually co-vary (Bergmann 1847, Stillwell et al. 2007), temperature is assumed to be a selective force producing Bergmann's rule. However, latitudinal clines in animals could also be caused by ecological or environmental factors that co-vary with latitude (Ashton 2002), such as moisture and humidity. Most studies assessing Bergmann's rule in animals have been from geographic zones with latitudes greater than 20 degrees (Zink and Remsen 1986, Graves 1991). Another body size pattern is Rensch's rule, which is an allometric law that states when males are the larger sex, sexual size dimorphism will increase with increasing body size, but when females are larger, sexual size dimorphism will decrease with increasing body size (Rensch 1960, Abouheif and Fairbairn 1997, Fairbairn 1997). An intraspecific version of Rensch's Rule says when males are the larger sex, male body size will vary more than female body size with respect to latitude (Blackenhorn et al. 2006). Few studies have been done discussing the relationship of sexual dimorphism with latitude (Graves 1991).

Here, I evaluate the extent of geographical variation in bill size and sexual size dimorphism across the range of a tropical montane bird, *Pseudocolaptes boissonneautii*. By doing so, I also examine whether body size follows Bergman's Rule and Rensch's Rule within this species. I discuss possible mechanisms underlying the evolution of sexual dimorphism and geographic variation in the degree of dimorphism in this tropical bird.

## Methods and Materials

### *Focal species*

*Pseudocolaptes boissonneautii* (Streaked Tuftedcheek) is a suboscine passerine bird in the family Furnariidae, the ovenbirds. It occurs in humid montane forests of the tropical Andes from Venezuela to Bolivia, where it usually occupies the upper understory and subcanopy where epiphytes are common (Remsen 2003, Schulenberg et al. 2007). As in many other montane forest Andean birds (Graves 1985, 1988), the geographic range of *P. boissonneautii* is long but narrow, extending for thousands of kilometers (approximately from 17 ° S to 10.5° N), but confined to a narrow elevational amplitude (between 1700 -3450 m) (Figure 1).



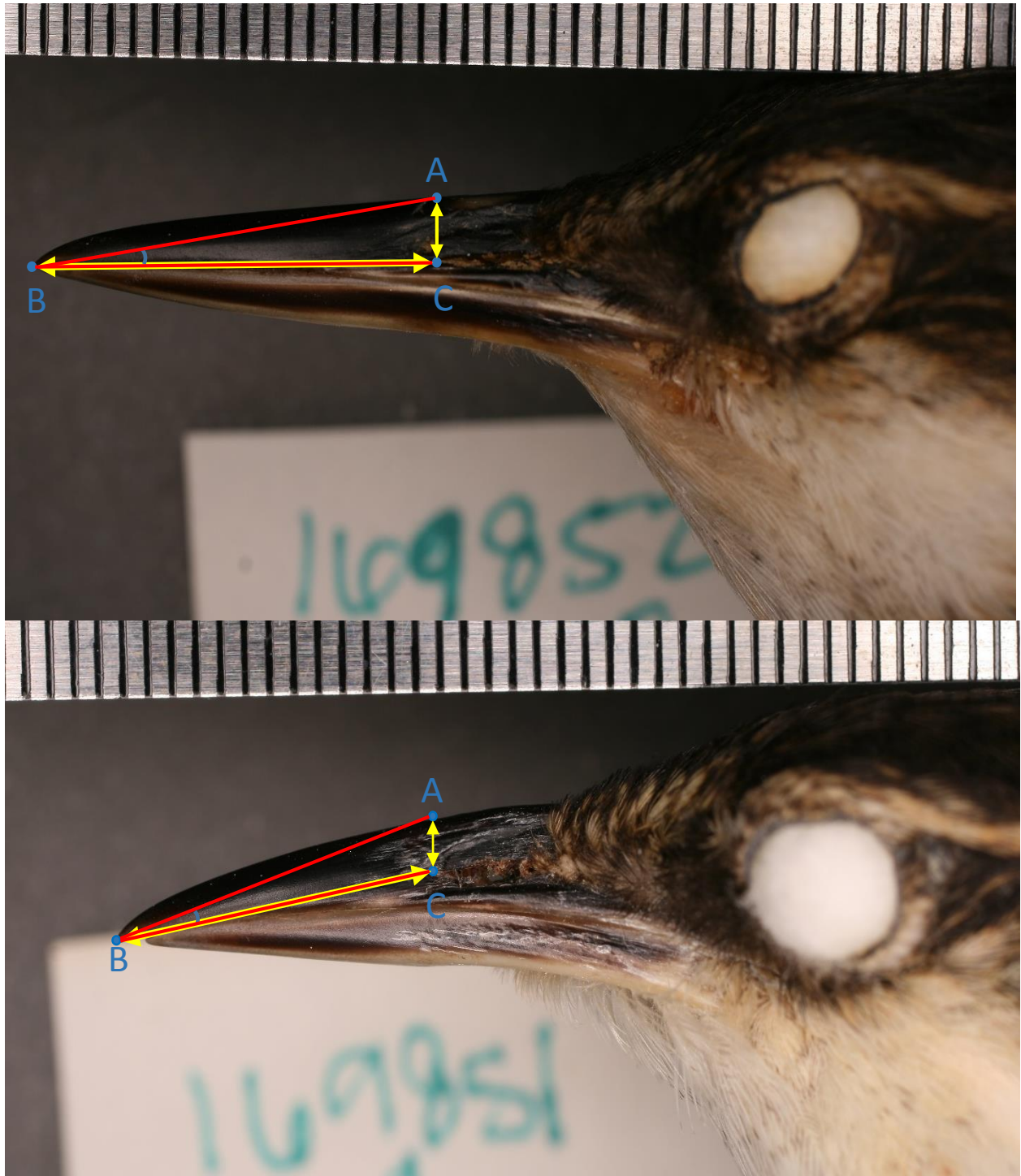
**Figure 1.** A) Geographic range of *Pseudocolaptes boissonneautii*. This species inhabits the humid slopes of tropical Andes from the northern coastal range of Venezuela south to the Bolivian Yungas. Map provided by Map of Life: <http://www.mol.org/>. B) This map depicts each individual specimen that I used in my study. The pink circle represents individuals for which wing and bill data were available, the blue

circles are wing specimens and the purple circles represent the specimens used for bill measurements. Map provided by <http://batchgeo.com/map/40a38a3d8e49504e191165e592670487>.

*Pseudocolaptes boissonneautii* is a medium-sized insectivorous bird that ranges in length between 20.5 cm and 21.5 cm in length, and weighs approximately 45-50 g (Remsen 2003). Similar to most furnariids, plumage patterns and coloration are identical in both sexes. However, females of *P. boissonneautii* have been noted to have longer bills than those of males (Zimmer 1936, Fjeldså and Krabbe 1990, Remsen 2003). Dimorphism in bill length has also been noted to be more pronounced in northern Peru in comparison to more southern populations (Schulenberg et al. 2007). However, little is known about the life history of *P. boissonneautii* or the extent of geographical variation in sexual dimorphism. This polytypic species consists of nine subspecies (Remsen 2003).

### ***Analysis***

I measured a total of 152 museum specimens of *P. boissonneautii* (83 females, 69 males), collected across the species geographic range (Fig.1B, Appendix A). Juveniles, unsexed specimens, and specimens with broken bills were excluded from analysis. For each specimen, I photographed the lateral side of the head and bill, with a metric scale for reference. I imported the files into ImageJ (Rasband 1997), placed three landmarks on the maxilla, and calculated the following measurements: (1) bill length (BL), from the anterior edge of nares to the tip of the bill; (2) the height of the maxilla (BH), from the culmen at the anterior edge of the nares to the maximum point of the culmen (on the same x-axis point as the anterior edge of the nares), and (3) an angle that describes the shape of the maxilla formed between the landmarks A to B and B to C (see Fig. 2).



**Figure 2.** Sample female (top) and male (bottom) *Pseudocolaptes boissonneautii* showing measurements taken from each specimen from three landmarks A, B, and C. Three measurements were taken: 1) bill length (BL) measured from point B to point C, maxilla height (BH) measured from point A to point C), and the angle (BA) formed at the common end point B, at the sides BA and BC.

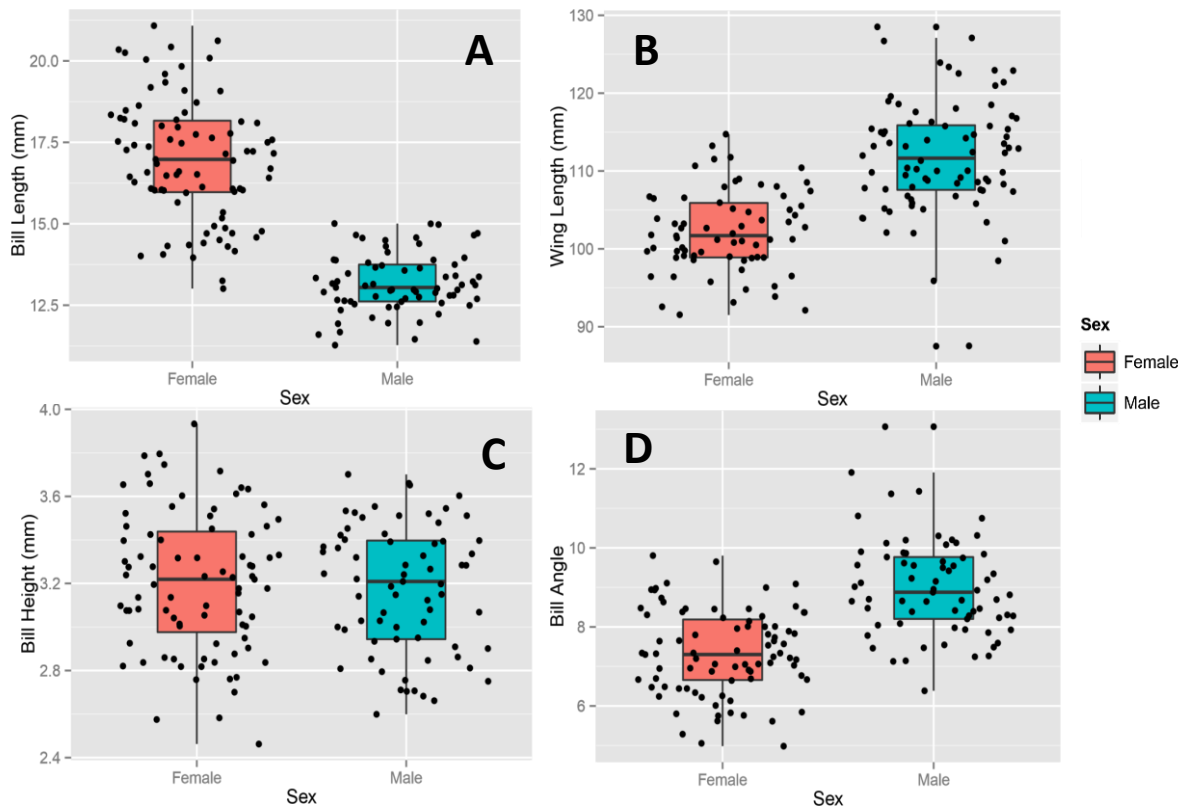


Each individual was measured twice, and the average of the two measurements was used for analysis. In addition, I analyzed wing length (taken as the wing chord in round skins) in *P. boissonneautii* for another set of 149 specimens to examine geographic variation in this trait and sexual size dimorphism. I used wing length as a surrogate for body size (Graves 1991) because most specimens did not have data on body weight. I extracted locality data from specimen labels and georeferenced each record using ornithological gazetteers (Paynter 1982, Paynter, Traylor & Winter 1975, Paynter & Traylor 1981, Stephens & Traylor 1983) and Google Earth.

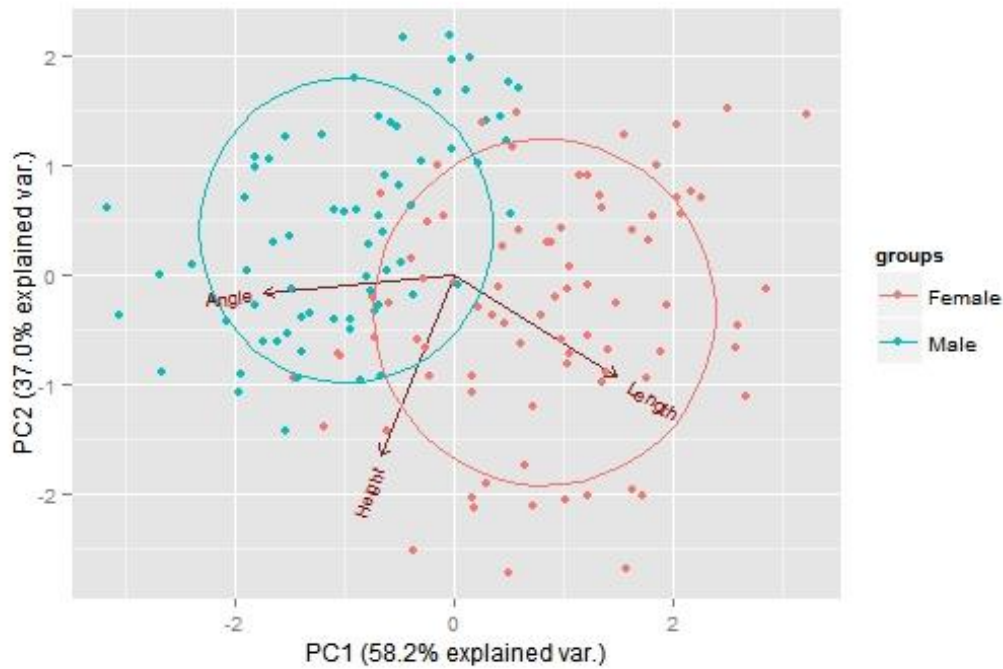
I examined sexual dimorphism in bill and wing length across the range of *P. boissonneautii*. First, I performed a Shapiro test of normality across all samples using raw data. Wing length ( $W = 0.99$ ,  $p = 0.53$ ), angle ( $W = 0.99$ ,  $p = 0.3$ ), and maxilla depth ( $W = 0.99$ ,  $p = 0.2$ ) were normally distributed, but bill length data ( $W = 0.95$ ,  $p < 0.001$ ) was not. Therefore, I compared difference in bill length using the non-parametric Mann-Whitney Wilcoxon test, but used t-tests for the other three traits. To further examine sexual dimorphism in bill size and shape, I conducted a Principal Component Analysis (PCA) on the three bill variables. To address the relationship between the traits, I performed linear regressions comparing bill length to wing length and angle to bill length. I then assessed latitudinal variation in sexual dimorphism in the four traits by conducting regression analysis using a Loess fit, which is a nonparametric tool used for fitting smooth curves (Jacoby 2000). I transformed bill length, wing length, and maxilla height using the natural log transformation before performing regression analysis; I did this because it normalizes the data. Statistical analysis were conducted in the program R (Team 2013); graphs were plotted using the “ggplot2” package in R (Wickham 2009).

## Results

*Pseudocolaptes boissonneautti* exhibited sexual dimorphism in bill length ( $W = 5547$ ,  $p < 0.00001$ ) and wing length ( $t = -9.38$ ,  $p < 0.00001$ ). Females on average had a significantly longer bill but shorter wing than males (Fig. 3). Males had a wider maxilla angle than females ( $t = -8.76$ ,  $p < 0.00001$ ), indicating a more curved culmen in the shorter bills of males, and straighter maxillas in the longer bills of females. The height of the maxilla did not differ significantly between sexes ( $t = 0.574$ ,  $p = 0.57$ ). Principal Component Analysis (PCA) also revealed sexual dimorphism in bill length and shape by using the three bill variables together (Fig. 4). PC1 accounted for 58.2% of the variance and PC2 accounted for 37.0% of variance.



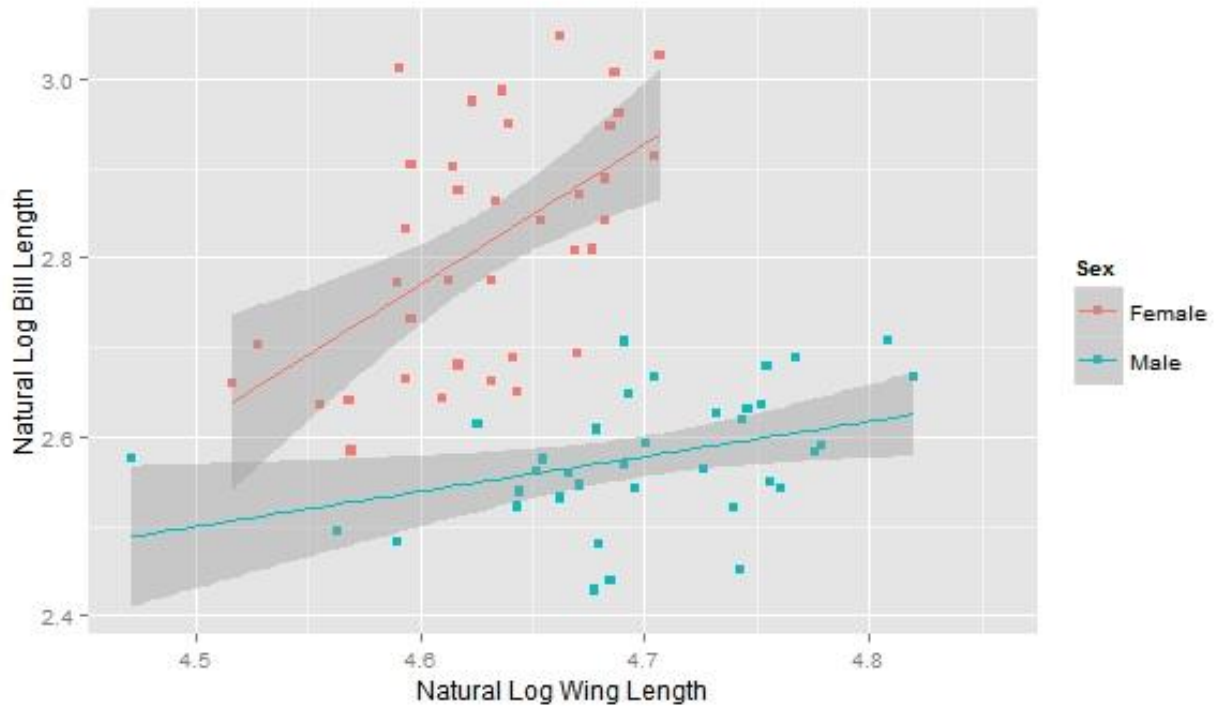
**Figure 3.** Sexual dimorphism in *Pseudocolaptes boissonneautii*: A) Bill length B) Wing length C) Maxilla Height and D) Bill Angle. Scatter points represent individual study specimens. The horizontal line represents the median size for the trait measured. The sample size for A, C, and D is 152 (83 females, 69 males). B has a sample size of 149 specimens (69 females, 80 males).



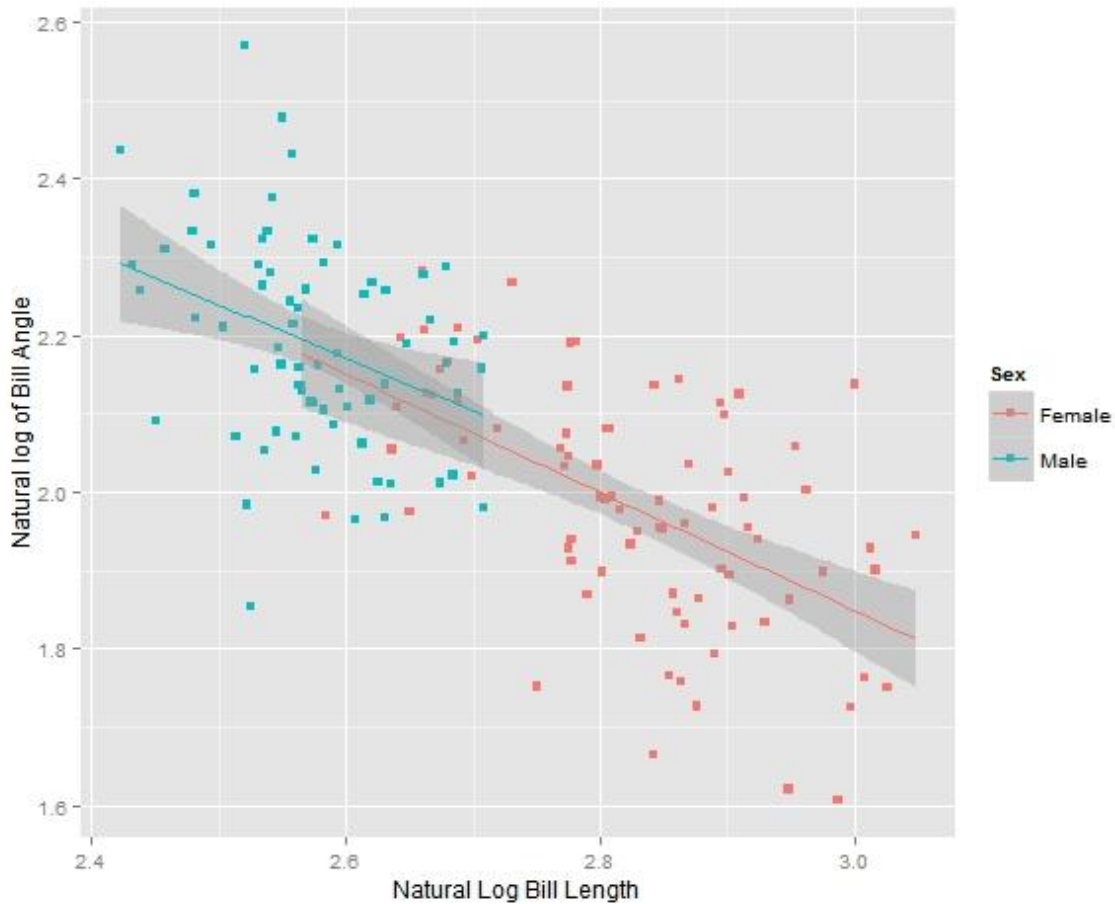
**Figure 4.** Principal components biplot showing sexual dimorphism in the bill of *Pseudocolaptes boissonneautii*. Data points color-coded by sex (females in pink, males in blue).

Analyses comparing the various traits measured showed that females ( $r^2 = 0.29$ ;  $p < 0.001$ ) had a steeper, more positive slope than males ( $r^2 = 0.12$ ;  $p < 0.05$ ) when comparing bill length to wing length using linear regressions (Fig. 5). Males are larger than females (Fig. 3B); however, body size is not as strongly correlated with bill length in males as it is in females; bill length and body size correlation is significant in both sexes. Bill angle was negatively correlated with bill length in both males ( $r^2 = 0.12$ ;  $p < 0.001$ ) and females ( $r^2 = 0.31$ ;  $p < 0.001$ ) (Fig. 6). In

both, slopes did not differ significantly, and the longer the length of the bill, the straighter the bill.



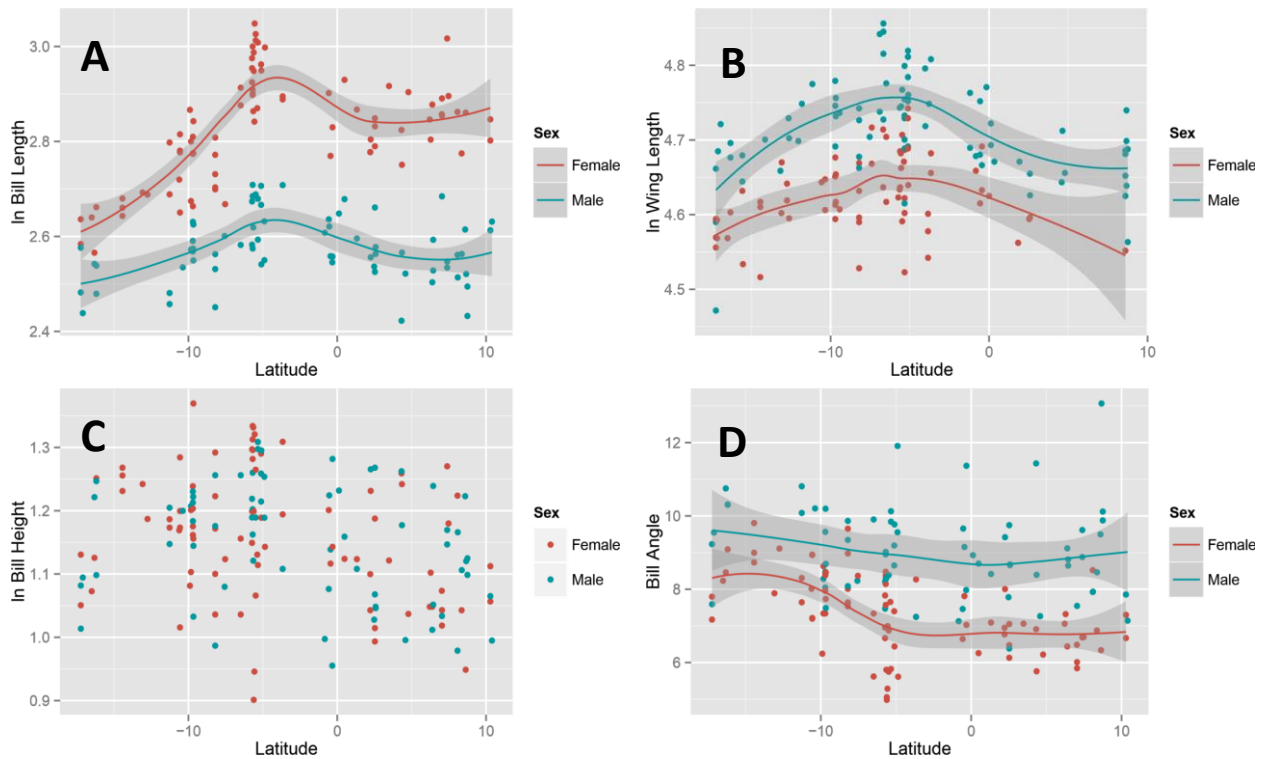
**Figure 5.** Linear regressions of the natural log of bill length compared to the natural log of wing length in males (blue) and females (pink) with a linear fit and the 95 % confidence region shaded in gray. Although bill length was positively correlated with wing length in both sexes, females displayed a stronger correlation.



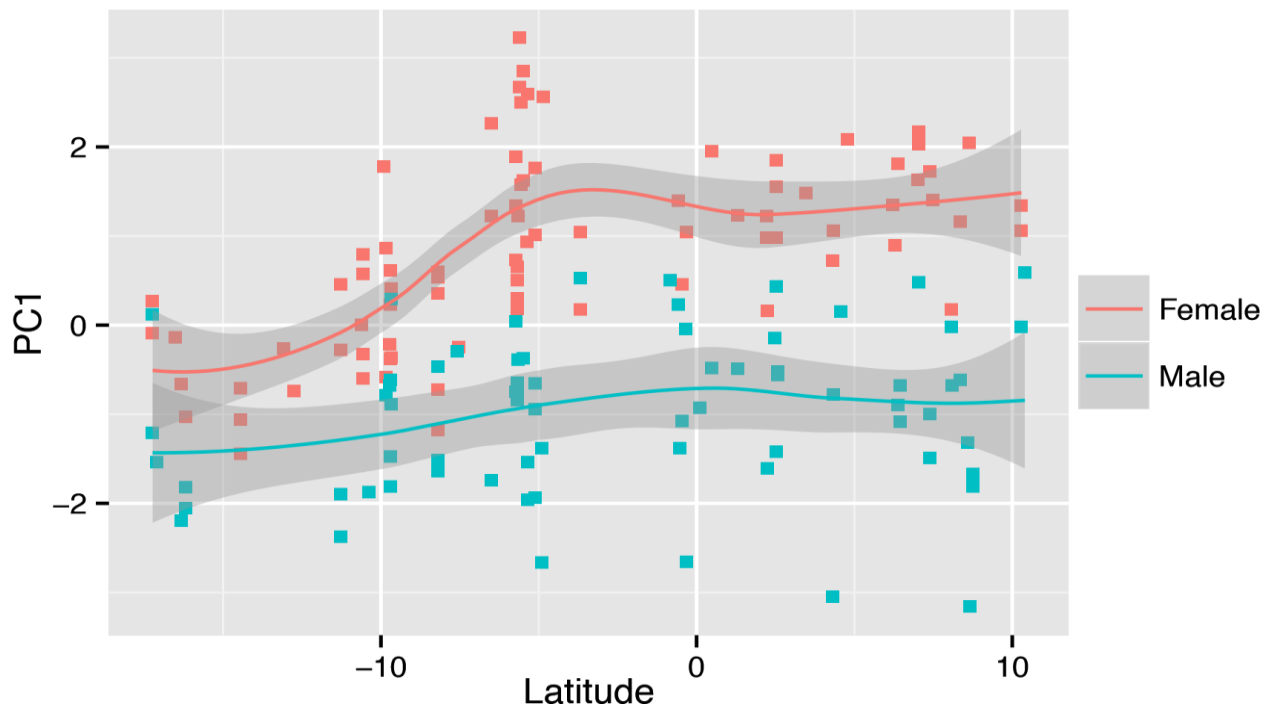
**Figure 6.** Linear regressions of bill angle compared to bill length in the study species in female and male *Pseudocolaptes boissonneautii* indicate a negative correlation between bill length and the curvature of the bill. The linear regressions are fitted with a 95% confidence interval, shaded in gray.

Bill length, and wing length showed latitudinal variation across the range of *Pseudocolaptes boissonneautii* (Fig. 7). Bill length increased towards the equator ( $\sim 5^\circ$  S), from both the northern ( $\sim 10^\circ$  N) and the southern ends of the range ( $\sim 17^\circ$ ). However, females showed a stronger degree of latitudinal variation than males; in fact, males did not significantly vary in bill size latitudinally despite their variation in body size. The southernmost population exhibit the smallest degree of dimorphism in this species. Latitudinal variation in wing length showed a

similar pattern to that of the bill, with the largest average values at the midpoint of the species range; however, unlike in the bill patterns, males on average were larger in size than females. Males did not vary significantly in bill angle geographically, but females in the south had more curved bills than in the rest of the geographic range (Fig. 7 D). Maxilla height did not show significant variation among males and females (Fig. 7 C). Latitudinal variation in dimorphism in bill size and shape is further described using the PC1 (Fig 8). Here, females displayed a stronger degree of latitudinal variation than males, females gradually increased whereas males remained relatively constant in size.



**Figure 7.** Geographic variation and sexual dimorphism in bill and wing size in male (blue) and female (pink) *Pseudocolaptes boissonneautti*. A). bill length, B). wing length, C). maxilla depth D). angle of the maxilla (see Fig. 2), Plots A, B, D are fitted with a Loess curve with a 95% confidence interval shade in gray. Plot C is not fitted with a line of best fit because no significant variation occurred between the sexes. Negative latitudes represent locations in the Southern Hemisphere. The sample size for A, C, and D is 152 (83 females, 69 males). B has a sample size of 149 specimens (69 females, 80 males).



**Figure 8.** Geographic variation in bill size and shape of *Pseudocolaptes boissonneautii*, as characterized by Principal Component 1. Females (pink, n= 83) show stronger latitudinal variation in bill morphology than males (blue, n=69). The scatterplot is fitted with a Loess curve and a 95% confidence region shaded in gray.

## Discussion

*What Drives Sexual Dimorphism?* – Males were found to be larger than females, but with shorter and more curved bills; however, females showed greater geographical variation in both bill morphology and wing length. Although it is evident that sexual dimorphism in bill morphology and wing length is present in *Pseudocolaptes boissonneautii*, the mechanisms driving it remains unclear. Although males were larger, females tended to have a longer, straighter bill than males. Males are larger than females in most species of birds (Amadon 1959), and small differences between males become extremely important in driving size dimorphism when sexual selection is present (Babbitt and Frederick 2007).

There are three nonexclusive hypotheses to consider when examining sexual dimorphism of bill morphology in birds (Lauro and Nol 1995). First, bill dimorphism may have evolved to reduce competition between limited resources such as food. Second, dimorphism may have arisen to increase partitioning of reproductive roles between sexes. Third, sexual dimorphism in bill length may arise from sexual selection, specifically male-male competition. However, there seems to be no sole cause for sexual dimorphism in bill morphology in groups of birds (Babbitt and Frederick 2007). For example, studies have suggested that in shorebirds (Szekely et al. 2000) bill dimorphism is not due to niche divergence in feeding habits, but in studies of other birds niche divergence drives bill dimorphism (Radford and Du Plessis 2004, Temeles and Kress 2003).

Species in the genus *Pseudocolaptes* forage on epiphytic bromeliads and other epiphytic substrates, such as on the lichen and moss layers of the trees of cloud forests (Zimmer 1936, Sillet 1994, Sillet et al. 1997). The diet of *P. boissonneautii* consists mostly of small vertebrates, and a variety of arthropods (Hilty 2003). Bromeliads can increase birds' chances for specialization and division of resources (Sillett 1994) because they create unique microhabitats for the birds and their prey (Sillett et al. 1997). Also, by males and females inhabiting different subniches or subzones, the total niche width used by the species is increased (Selander 1966). Specialization of different foraging techniques decreases intersexual competition for food (Radford and du Plessis 2003). If foraging and diet segregation between sexes is a possible mechanism driving sexual dimorphism in *P. boissonneautii*, then females may have evolved their longer and straighter bills to feed on bromeliads of different sizes and structures than their males counter parts, the bill of which remain constant in length throughout the species' range. For instance, females could use their bills to probe deeper into the bromeliad than males. Food



preference could also cause a dimorphism of feeding parts (Temeles and Kress 2003). Males and females could take different prey. It is also probable that the sexes specialize on the types of foraging strata, meaning that the sexes feed from different species of bromeliads. For example, the Caribbean purple-throated carib hummingbird displays sexual dimorphism in bill morphology that is associated with floral dimorphism in the *Heliconia* plants it feeds from. If the latter foraging-related hypothesis are true, I predict that careful natural history observation on the foraging behavior of this species would show greater divergence in behavior between sexes at the midpoint of the species range since males and females; the sexes show greater bill dimorphism at this point in the range. However, it is difficult to confirm that sexual dimorphism in bill shape and size is due to differences in ecology and uses of resources alone, because differences in trophic structures often correlate positively with body size in animals (Temeles 2000). This positive correlation makes it uncertain whether these ecological differences between the males and females are the consequence or the cause of sexual dimorphism (Temeles 2000). The second hypothesis to explain bill morphology in birds is that females and males could also use their bills differently in parenting and nest building (Lauro and Nol 1995). However, sexual dimorphism in bill length and shape are unlikely to be due to parental care because *Pseudocolaptes* species use natural cavities, particularly those created by woodpeckers in tree trunks, so birds do not need to excavate nests (Radford and Du Plessis 2004). The breeding behavior of *P. boissonneautii* has yet to be studied in detail. Sexual selection is a third hypotheses for the causation of bill dimorphism in birds, but may not be the cause in the case of *P. boissonneautii* because females displayed a greater degree of variation in bill morphology than males. However, sexual selection may be acting on body size to cause SSD considering that males and females displayed sexual differences in size where males were larger. Sexual selection

often selects for larger males either through male-male competition or female mate choice (Darwin 1874, Andersson 1994). Because little is known about the natural history of *P. boissonneautii* it is difficult to examine these hypotheses any further. To distinguish which factors are the leading forces in sexual dimorphism in *Pseudocolaptes boissonneautii*, fieldwork needs to be done observing foraging behavior and feeding ecology as well as breeding behavior.

*Geographical variation*- The data collected for latitudinal variation (Fig. 7) does not support Bergmann's rule because body size is not positively correlated with latitude throughout the entire range of *Pseudocolaptes boissonneautii*. Although birds often have a larger body size at higher latitudes (Ashton 2002), the trend was for body size in *P. boissonneautii* was to increase towards the midpoint of the range (~5° South). Bill and wing length was largest in both sexes of *Pseudocolaptes boissonneautii* near the midpoint of the range. Individuals of both sexes from the south have more curved, shorter bills and are less sexually dimorphic than elsewhere in its range. The latitudinal (geographical) increase in body size covaried strongly with bill size in females, but not in males; larger males had approximately the same size bill as smaller males. The data also does not conform to Rensch's rule. In the case of *Pseudocolaptes boissonneautii*, females displayed a greater body size divergence and expressed a larger variance of bill length size than males even though males were the larger sex.

## **Conclusion**

In this study, I analyzed the extent of sexual dimorphism in bill morphology, wing length, and ultimately sexual size dimorphism in *Pseudocolaptes boissonneautii*, and demonstrated that the degree of dimorphism varies geographically. Overall, females had a longer and straighter bill

than males. However they had a smaller wing length, indicating a smaller body size.

Geographical variation in this species does not conform to Bergmann's rule or Rensch's rule.

*Pseudocolaptes boissonneautii* has not been studied extensively so it is not known why sexual dimorphism in bill size and shape occurs, but there are a various hypotheses. Dimorphism could have arisen from ecological causes alone or through interactions with sexual selection. Further research and studies (i.e. phylogenetic analysis) are needed to determine the cause of geographical variation in sexual dimorphism in the montane bird *Pseudocolaptes boissonneautii*. There was a larger sample size from Peru; if more specimens were collected from the rest of the range then the data could possibly shift.

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**Appendix A.** Bill and wing length specimens used in this study are shown. Specimens for which both wing length and bill length were available are denoted by an asterisk (\*) next to the museum. The following museums loaned specimens: American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Louisiana State University (LSU), U.S. National Museum of Natural History (USNM), and Mississippi Museum of Natural Science (MS). For sex, F represents females while M represents males.

Museum	Catalog number	Country	State	Locality	Latitude	Sex
<b>* FMNH</b>	180337	Bolivia	Cochabamba	Incachaca	-17.23	F
<b>*FMNH</b>	180338	Bolivia	Cochabamba	Incachaca	-17.23	F
<b>FMNH</b>	180339	Bolivia	Cochabamba	Incachaca	-17.23	F
<b>*FMNH</b>	180340	Bolivia	Cochabamba	Incachaca	-17.23	M
<b>*FMNH</b>	180343	Bolivia	Cochabamba	Incachaca	-17.23	M
<b>*FMNH</b>	180344	Bolivia	Cochabamba	Incachaca	-17.23	M
<b>FMNH</b>	180342	Bolivia	Cochabamba	El Palmar, Yungas	-17.21	M
<b>LSU</b>	36053	Bolivia	La Paz - Coch	El Limbo	-17.16	F
<b>LSU</b>	36054	Bolivia	La Paz - Coch	El Limbo	-17.16	F
<b>FMNH</b>	217688	Bolivia	Cochabamba	Ayopaya; Bajo Choro	-16.93	M
<b>* LSU</b>	37648	Bolivia	Cochabamba	Ayopaya; Bajo Choro	-16.50	F
<b>LSU</b>	102017	Bolivia	La Paz - Coch	Chuspipata	-16.32	F

<b>*LSU</b>	102016	Bolivia	La Paz - Coch	Chusipata	-16.32	M
<b>LSU</b>	102018	Bolivia	La Paz - Coch	Chusipata	-16.32	M
<b>LSU</b>	102019	Bolivia	La Paz	Ca 1 km S Chusipata	-16.32	F
<b>*LSU</b>	96000	Bolivia	La Paz	Cotapata, 4.5 km WNW Chusipata	-16.19	F
<b>*LSU</b>	95998	Bolivia	La Paz	Cotapata, 4.5 km WNW Chusipata	-16.19	M
<b>*LSU</b>	95999	Bolivia	La Paz	Cotapata, 4.5 km WNW Chusipata	-16.19	M
<b>LSU</b>	37647	Bolivia	La Paz - Coch	Alto Palmar	-15.53	F
<b>*LSU</b>	98289	Peru	Puno	Valcon, 5 km NNW Quiaca	-14.43	F
<b>*LSU</b>	98290	Peru	Puno	Valcon, 5 km NNW Quiaca	-14.43	F
<b>*LSU</b>	98293	Peru	Puno	Valcon, 5 km NNW Quiaca	-14.43	F
<b>AMNH</b>	149909	Peru		below Limbani	-14.13	M
<b>AMNH</b>	166541	Peru	Torontoy		-13.17	M
<b>FMNH</b>	299588	Peru	Cuzco	Bosque San Luis	-13.1	F
<b>*LSU</b>	78375	Peru	Cusco Dept.	14 km NE Abra Malaga on Ollantaitambo-Quillabamba Rd.	-13.08	F
<b>LSU</b>	78376	Peru	Cusco Dept.	14 km NE Abra Malaga on Ollantaitambo-Quillabamba Rd.	-13.08	F
<b>*LSU</b>	69432	Peru	Ayacucho Dept.	Yuraccyacu	-12.75	F
<b>AMNH</b>	820779	Peru	Ayacucho	Yuraccyacu	-12.75	F
<b>LSU</b>	820054	Peru	Cuzco	Vilcabamba	-12.62	M
<b>LSU</b>	820420	Peru	Cuzco	Vilcabamba	-12.62	F
<b>LSU</b>	820474	Peru	Cuzco	Vilcabamba	-12.62	M
<b>AMNH</b>	169755	Peru	Junin	Maraynioc	-12.03	M

<b>AMNH</b>	169756	Peru	Junin	Cheroes	-11.81	M
<b>LSU</b>	127636	Peru	Junin	Via Satipo, Chanchuleo, ca 8 km SE Calabaza	-11.27	F
<b>LSU</b>	127639	Peru	Junin	Via Satipo, Chanchuleo, ca 8 km SE Calabaza	-11.27	F
<b>LSU</b>	127638	Peru	Junin	Via Satipo, Chanchuleo, ca 8 km SE Calabaza	-11.27	M
<b>LSU</b>	127641	Peru	Junin	Via Satipo, Chanchuleo, ca 8 km SE Calabaza	-11.27	M
<b>AMNH</b>	235537	Peru	San Pedro	S Chachapoyas	-11.15	M
<b>LSU</b>	105939	Peru	Pasco	Santa Cruz, ca 9 Km SSE Oxapampa	-10.62	F
<b>LSU</b>	105940	Peru	Pasco	Cumbre de Ollon, ca 12 Km E Oxapampa	-10.57	F
<b>LSU</b>	105941	Peru	Pasco	Cumbre de Ollon, ca 12 Km E Oxapampa	-10.57	F
<b>LSU</b>	105942	Peru	Cusco Dept.	Cumbre de Ollon, ca 12 Km E Oxapampa	-10.57	F
<b>LSU</b>	128497	Peru	Huánuco	Millpo, E Tambo de Vacas on Pozuzo-Chaglla trail	-10.38	M
<b>MS</b>	1178	Peru	Huánuco	Ollon	-10.34	F
<b>LSU</b>	113572	Peru	Pasco	Bosque Potrero, 14 km W Pano	-9.9	F
<b>LSU</b>	128495	Peru	Pasco	Playa Pampa, ca 8 km NW Cushi on trail to Chaglla	-9.83	F
<b>LSU</b>	128496	Peru	Pasco	Playa Pampa, ca 8 km NW Cushi on trail to Chaglla	-9.83	F
<b>LSU</b>	128494	Peru	Pasco	Playa Pampa, ca 8 km NW Cushi on trail to Chaglla	-9.83	M
<b>*LSU</b>	62267	Peru	Huánuco	E slope Cordillera Carpish, Carretera Central	-9.70483	F
<b>*LSU</b>	64156	Peru	Huánuco Dept.	E slope Cordillera Carpish, Carretera Central	-9.70	M
<b>*LSU</b>	74036	Peru	Huánuco Dept.	Bosque Cutirragra S. Huaylaspampa	-9.70	F
<b>*LSU</b>	74039	Peru	Huánuco Dept.	Bosque Cutirragra S. Huaylaspampa	-9.70	F

<b>*LSU</b>	74040	Peru	Huánuco Dept.	Bosque Huaylaspampa	-9.70	F
<b>*LSU</b>	74037	Peru	Huánuco Dept.	Bosque Cutirragra S. Huaylaspampa	-9.70	M
<b>*LSU</b>	74038	Peru	Huánuco Dept.	Bosque Cutirragra S. Huaylaspampa	-9.70	M
<b>LSU</b>	119008	Peru	Huánuco Dept.	Unchog, pass between Churubamba and Hda Paty, NNW Acomayo	-9.68	M
<b>*LSU</b>	74035	Peru	Huánuco Dept.	Trail to Hda. Paty below Carpish Pass	-9.67	F
<b>*LSU</b>	74045	Peru	Huánuco Dept.	Bosque Magra Pampa below Zapatogocha	-9.67	F
<b>DW</b>	64157	Peru	Huánuco Dept.	Carpish	-9.7	M
<b>LSU</b>	74041	Peru	Huánuco Dept.	Base of Bosque Zapatogocha above Acomayo	-9.67	M
<b>LSU</b>	74044	Peru	Huánuco Dept.	E forest between Zapatogocha & Huaylaspampa	-9.67	M
<b>AMNH</b>	820956	Peru	Huánuco	Sira	-9.43	F
<b>AMNH</b>	820955	Peru	Huánuco	Sira	-9.43	M
<b>*LSU</b>	92263	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	F
<b>*LSU</b>	92266	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	F
<b>LSU</b>	92268	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	F
<b>*LSU</b>	92270	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	F
<b>*LSU</b>	92272	Peru	La Libertad	Mashua, E Tayabamba, on trail to Ongon	-8.2	F
<b>*LSU</b>	92265	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	M

<b>*LSU</b>	92267	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	M
<b>*LSU</b>	92269	Peru	La Libertad	Cumpang, above Utcubamba, on trail to Ongon	-8.2	M
<b>LSU</b>	170832	Peru	Loreto	Ca. 85 km SE Juanjui	-7.57	M
<b>*LSU</b>	104483	Peru	San Martin	Puerta del Monte, ca 30 km NE Los Alisos	-7.53	F
<b>AMNH</b>	235918	Peru	Taulis	Pacasmayo	-7.4	F
<b>AMNH</b>	235919	Peru	Taulis	Pacasmayo	-7.4	F
<b>AMNH</b>	235916	Peru	Taulis	NE Pacasmayo	-6.9	M
<b>AMNH</b>	235917	Peru	Taulis	NE Pacasmayo	-6.9	M
<b>AMNH</b>	524083			Leimabamba	-6.68	F
<b>AMNH</b>	524086			Leimabamba	-6.68	F
<b>AMNH</b>	235920	Peru	Chugur		-6.67	M
<b>AMNH</b>	235921	Peru	Chugur		-6.67	M
<b>AMNH</b>	235922	Peru	Chugur		-6.67	M
<b>AMNH</b>	235923	Peru	Chugur		-6.67	M
<b>*LSU</b>	84703	Peru	Cajamarca Dept.	7 km N, 3 km E Chota	-6.49	F
<b>*LSU</b>	84704	Peru	Cajamarca Dept.	7 km N, 3 km E Chota	-6.49	F
<b>*LSU</b>	84705	Peru	Cajamarca Dept.	7 km N, 3 km E Chota	-6.49	M
<b>*LSU</b>	81936	Peru	Amazonas Dept.	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.73	F
<b>LSU</b>	173952	Peru	San Martin	Quebrada Lanchal, ca. 8 km ESE Sallique	-5.72	F
<b>LSU</b>	173954	Peru	San Martin	Quebrada Lanchal, ca. 8 km ESE Sallique	-5.72	F
<b>LSU</b>	173951	Peru	San Martin	Quebrada Lanchal, ca. 8 km ESE Sallique	-5.72	M

<b>LSU</b>	173953	Peru	San Martin	Quebrada Lanchal, ca. 8 km ESE Sallique	-5.72	M
<b>LSU</b>	169852	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	F
<b>LSU</b>	169853	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	F
<b>LSU</b>	169856	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	F
<b>LSU</b>	169857	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	F
<b>LSU</b>	169851	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	M
<b>LSU</b>	169854	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	M
<b>LSU</b>	169855	Peru	Cajamarca	33 rd. km NE Ingenio on rd. to Laguna Pomacochas	-5.68	M
<b>*LSU</b>	87860	Peru	Amazonas	SE La Peca	-5.64	F
<b>*LSU</b>	87859	Peru	Amazonas	SE La Peca	-5.64	M
<b>*LSU</b>	87854	Peru	Amazonas	20 trail km E La Peca	-5.61	F
<b>*LSU</b>	87855	Peru	Amazonas	20 trail km E La Peca	-5.61	F
<b>*LSU</b>	80552	Peru	Amazonas	404 km on Balsas-Leymebamba rd, Utcubamba drainage	-5.57	F
<b>*LSU</b>	87861	Peru	Amazonas	Cordillera Colan, SE La Peca	-5.55	F
<b>LSU</b>	87862	Peru	Amazonas	Colan	-5.55	M
<b>*LSU</b>	87856	Peru	Amazonas	Cordillera Colan, SE La Peca	-5.48	F
<b>*LSU</b>	87857	Peru	Amazonas	Cordillera Colan, SE La Peca	-5.48	F
<b>*LSU</b>	87858	Peru	Amazonas	Cordillera Colan, SE La Peca	-5.48	M
<b>AMNH</b>	175312	Peru	Piura	Palambla	-5.383	M

<b>*LSU</b>	80550	Peru	Piura Dept.	W side of Pass between Canchaque and Huancabamba	-5.37	F
<b>*LSU</b>	97666	Peru	Piura	Cruz Blanca, 33 road km SW Huancabamba	-5.33	F
<b>LSU</b>	127637	Peru				
<b>*LSU</b>	78374	Peru	Piura Dept.	33 road km SW Huancabamba	-5.33	M
<b>LSU</b>	80551	Peru				
<b>*LSU</b>	97667	Peru	Piura	Cruz Blanca, 33 road km SW Huancabamba	-5.33	M
<b>MS</b>	1146	Peru	Huanuco - Pasco	Sta Cruz	-5.33	F
<b>LSU</b>	127640	Peru	Junin	Chanchuleo	-5.33	M
<b>*LSU</b>	97668	Peru	Piura/ Cajamarca	Cerro Chinguela, 5 km NE Sapalache	-5.12	M
<b>*LSU</b>	87852	Peru	Cajamarca Dept./Piura Dept.	Cerro Chinguela, 5 km NE Sapalache	-5.12	F
<b>*LSU</b>	87853	Peru	Cajamarca Dept./Piura Dept.	Cerro Chinguela, 5 km NE Sapalache	-5.12	M
<b>AMNH</b>	234718	Peru	La Lejia	N Chachapoyas	-5.12	F
<b>AMNH</b>	234719	Peru	La Lejia	N Chachapoyas	-5.12	F
<b>AMNH</b>	234715	Peru	La Lejia	N Chachapoyas	-5.12	M
<b>AMNH</b>	234716	Peru	La Lejia	N Chachapoyas	-5.12	M
<b>AMNH</b>	234717	Peru	La Lejia	N Chachapoyas	-5.12	M
<b>AMNH</b>	234720	Peru	La Lejia	N Chachapoyas	-5.12	M
<b>*LSU</b>	81935	Peru	Cajamarca Dept./Piura Dept.	Above San Jose de Lourdes East side of Ridge	-5.10	F
<b>*LSU</b>	81934	Peru	Cajamarca Dept./Piura Dept.	E side ridge E above San Jose do Lourdes	-5.10	M

<b>LSU</b>	178990	Peru	Cajamarca Dept./Piura Dept.	Hito Jesus	-4.9	M
<b>LSU</b>	178988	Peru	Cajamarca Dept./Piura Dept.	Ca. 2 km WSW Hito Jesus	-4.89	M
<b>LSU</b>	178989	Peru	Cajamarca Dept./Piura Dept.	4.5 km NNW Hito Jesus	-4.86	F
<b>AMNH</b>	146180	Peru		Santa Domingo	-3.85	F
<b>AMNH</b>	146181	Peru		Santa Domingo	-3.85	F
<b>AMNH</b>	146182	Peru		Santa Domingo	-3.85	F
<b>AMNH</b>	167339	Ecuador	Oro	Salvias	-3.78	
<b>*AMNH</b>	167335	Ecuador	Oro	Taraguacocha	-3.67	F
<b>*AMNH</b>	167336	Ecuador	Oro	Taraguacocha	-3.67	F
<b>*AMNH</b>	167337	Ecuador	Taraguacoch a	Prov. Del Oro.	-3.67	M
<b>ANMH</b>	524080	Ecuador		Paramo de Corazon	-1.2	M
<b>AMNH</b>	524078	Ecuador		Valle de Viciosa	-0.83	
<b>*AMNH</b>	524077	Ecuador		Viciosa Valley	-0.83	M
<b>*AMNH</b>	186387	Ecuador		Sumaco Arriba	-0.57	F
<b>AMNH</b>	184318	Ecuador		Sumaco Arriba	-0.57	M
<b>*AMNH</b>	184320	Ecuador		Sumaco Arriba	-0.57	M
<b>*AMNH</b>	524082	Ecuador		Corazon	-0.53	M
<b>*AMNH</b>	173785	Ecuador		Beaza, Arriba	-0.45	F
<b>*AMNH</b>	173783	Ecuador		Beaza, Arriba	-0.45	M



<b>AMNH</b>	176081	Ecuador		Beaza, Arriba	-0.45	F
<b>*AMNH</b>	524079	Ecuador		Guamani Pass	-0.33	M
<b>*AMNH</b>	524075	Ecuador	Pichincha		-0.32	F
<b>*AMNH</b>	180324	Ecuador	Pichincha		-0.32	M
<b>*AMNH</b>	124517	Ecuador	Pichincha	Gualea	0.12	M
<b>AMNH</b>	173054	Ecuador	Pichincha	W side Pichincha	0.12	
<b>FMNH</b>	292106	Colombia	Nariño	Llorente	0.49	F
<b>FMNH</b>	292105	Colombia	Nariño	Llorente	0.49	M
<b>FMNH</b>	292110	Colombia	Nariño	La Victoria	1.32	F
<b>FMNH</b>	292109	Colombia	Nariño	La Victoria	1.32	M
<b>AMNH</b>	116383	Colombia	Huila	La Candela	1.83	F
<b>AMNH</b>	116381	Colombia	Quindio	Almaguer	1.92	M
<b>USNM</b>	446549	Colombia	Huila	Tijeras, Moscopan	2.22	F
<b>FMNH</b>	249690	Colombia	Huila	Tijeras	2.22	F
<b>ANSP</b>	144338	Colombia	Cauca	Munchique; El Tambo	2.25	F
<b>ANSP</b>	144336	Colombia	Cauca	Munchique; El Tambo	2.25	M
<b>LSU</b>	45349	Colombia	Cauca	Malvase	2.48	M
<b>LSU</b>	38665	Colombia	Cauca	Cerro Munchique	2.53	F
<b>AMNH</b>	109661	Colombia	Cauca	Cerro Munchique	2.53	F
<b>AMNH</b>	226602	Colombia	Cauca	Cerro Munchique	2.53	F
<b>LSU</b>	38656	Colombia	Cauca	Cerro Munchique	2.53	M
<b>FMNH</b>	226603	Colombia	Cauca	Cerro Munchique	2.53	M

<b>*FMNH</b>	51033	Colombia	Cauca	Coast Range W. of Popayan	2.58	M
<b>FMNH</b>	51034	Colombia	Cauca	Coast Range W. of Popayan	2.58	F
<b>*AMNH</b>	109665	Colombia	Cauca	La Florida	2.58	M
<b>AMNH</b>	109659	Colombia	Cauca	Coast Range	3.48	F
<b>ANSP</b>	153884	Colombia	Tolima	Toche	4.32	F
<b>ANSP</b>	153883	Colombia	Tolima	Toche	4.32	M
<b>ANSP</b>	153887	Colombia	Caldas	La Guneta	4.35	F
<b>ANSP</b>	153886	Colombia	Caldas	La Guneta	4.35	M
<b>*AMNH</b>	112077	Colombia	Cauca	La Guneta	4.58	M
<b>AMNH</b>	112080	Colombia	Cauca	above Salento	4.63	M
<b>AMNH</b>	112075	Colombia	Quindio	Santa Isabel	4.78	M
<b>AMNH</b>	112076	Colombia	Quindio	Santa Isabel	4.78	F
<b>AMNH</b>	133561	Colombia	Antioquia	Santa Elena	6.22	F
<b>USNM</b>	436420	Colombia	Antioquia	Paramo de Frontino	6.28	F
<b>USNM</b>	426105	Colombia	Antioquia	Hacienda Potreros, 15 mi SW Frontino, Rio Herradura	6.39	F
<b>USNM</b>	426107	Colombia	Antioquia	Hacienda Potreros, 15 mi SW Frontino, Rio Herradura	6.39	M
<b>ANSP</b>	66439	Colombia	Santander	La Pica	6.45	M
<b>ANSP</b>	66438	Colombia	Santander	La Pica	6.45	M
<b>FMNH</b>	261307	Colombia	Boyaca	Hacienda La Primavera, Rio Cubugon	7.03	F
<b>USNM</b>	411175	Colombia	Santander	Hacienda Las Vegas, 12 mi up valley from Piedecuesta	7.04	F
<b>USNM</b>	411177	Colombia	Santander	Hacienda Las Vegas, 12 mi up valley from Piedecuesta	7.04	F

<b>USNM</b>	411176	Colombia	Santander	Hacienda Las Vegas, 12 mi up valley from Piedecuesta	7.04	M
<b>FMNH</b>	43520	Colombia	Norte de Santander	Paramo de Tama	7.39	F
<b>FMNH</b>	43518	Colombia	Norte de Santander	Paramo de Tama	7.39	M
<b>FMNH</b>	43519	Colombia	Norte de Santander	Paramo de Tama	7.39	M
<b>ANSP</b>	66441	Colombia	Santander	Ramiriz	7.48	F
<b>AMNH</b>	524058	Venezuela		La Culata	8.08	F
<b>*AMNH</b>	524057	Venezuela		La Culata	8.08	M
<b>USNM</b>	392666	Colombia		Alto Del Pozo, Highway Abrego - Sardinata	8.1	M
<b>FMNH</b>	53906	Venezuela		Rio Mucujun	8.36	F
<b>USNM</b>	392665	Colombia		Alto Del Pozo, Highway Abrego - Sardinata	8.37	M
<b>*AMNH</b>	524054	Venezuela	Merida	El Escorial	8.6	M
<b>AMNH</b>	524055	Venezuela	Merida	El Escorial	8.6	F
<b>AMNH</b>	524053	Venezuela	Merida	El Escorial	8.6	M
<b>AMNH</b>	100750	Venezuela	Merida	El Escorial	8.6	M
<b>FMNH</b>	152304	Venezuela	Merida	Escorial	8.63	F
<b>AMNH</b>	100751	Venezuela	Merida	El Valle	8.67	M
<b>AMNH</b>	524051	Venezuela	Merida	El Valle	8.67	M
<b>*AMNH</b>	524052	Venezuela	Merida	El Valle	8.67	M
<b>USNM</b>	190381	Venezuela		Culata	8.75	M
<b>AMNH</b>	131217	Venezuela	Merida	Culata	8.75	M
<b>*AMNH</b>	524059	Venezuela		La Culata	8.75	M

<b>USNM</b>	373249	Colombia		Laguna de Junco, At foot of Cerro Pintado, Sierra Perija	10.29	F
<b>USNM</b>	373251	Colombia		Laguna de Junco, At foot of Cerro Pintado, Sierra Perija	10.29	F
<b>USNM</b>	373255	Colombia		Laguna de Junco, At foot of Cerro Pintado, Sierra Perija	10.29	M
<b>USNM</b>	444218	Venezuela		Colonia Tovar	10.4	M