

**BIOMETRY OF TWO SYMPATRIC SPECIES OF THE GENUS *HYPOCNEMIS* (AVES: THAMNOPHILIDAE) IN SOUTHWESTERN AMAZONIA**Diego Pedroza¹ · Edson Guilherme²

¹Programa de Pós-Graduação em Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre (UFAC), Caixa Postal 500, 69920-900, Rio Branco, AC, Brazil.

²Centro de Ciências Biológicas e da Natureza, UFAC, Caixa Postal 500, 69920-900, Rio Branco, AC, Brazil.

E-mail: Diego Pedroza · diego.guima1@hotmail.com

Abstract · Differences in size and shape between sympatric congener species may affect their dominance interactions. In Amazonia, the Peruvian Warbling-Antbird (*Hypocnemis peruviana*) is partly sympatric with the Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*). Here, we investigated whether biometric differences exist between *H. peruviana* and *H. subflava*, and whether the species are sexually dimorphic. We measured 10 biometric traits in 52 individuals (24 *H. peruviana* and 28 *H. subflava*). From the analyses, we conclude that *H. peruviana* is slightly larger than *H. subflava* and that this may reflect a certain competitive dominance of the former over the latter. Some biometric traits were also different between the sexes in both species, which may minimize the competition for resources between the sexes.

Resumo · **Biometria de duas espécies simpátricas do gênero *Hypocnemis* (Aves: Thamnophilidae) no sudoeste da Amazônia**

diferenças no tamanho e na forma entre espécies congêneres simpátricas podem afetar as interações de dominância dessas espécies. Na Amazônia, parte da distribuição do cantador-sinaleiro (*Hypocnemis peruviana*) encontra-se em simpatria à distribuição do cantador-galego (*H. subflava*). Nosso objetivo foi saber se há diferenças biométricas entre *H. peruviana* e *H. subflava* e entre os sexos de ambas espécies. Nós medimos 10 traços biométricos em 52 indivíduos (24 *H. peruviana* and 28 *H. subflava*). A partir das análises concluímos que *H. peruviana* é ligeiramente maior que *H. subflava* e que isso pode indicar uma certa dominância competitiva de uma espécie sobre a outra. Entre os sexos de ambas as espécies, alguns traços biométricos se diferem e isso pode minimizar a competição por recursos entre os sexos.

Key words: Acre · Biometric asymmetry · Brazil · Morphometry · Sexual dimorphism

INTRODUCTION

Two species of the genus *Hypocnemis*—the Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and the Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*)—occur in sympatry in southwestern Amazonia (Isler et al. 2007). *H. peruviana* is widely distributed in the Amazon basin, between the left margin of the Madeira River and the foothills of the Andes, in Bolivia and Peru, including most of the Brazilian state of Amazonas, and all of Acre (Isler et al. 2007). *H. subflava* is found within a much smaller area, ranging between eastern Acre, in Brazil, to the Andean foothills in Bolivia and Peru, and is thus restricted to only a part of southwestern Amazonia (Isler et al. 2007, Tobias & Seddon 2009). *H. peruviana* is found in both várzea swamps and terra firme forests, and occurs occasionally in bamboo habitats (or patches) in southwestern Amazonia (Isler et al. 2007, Tobias & Seddon 2009, Guilherme 2016). By contrast, *H. subflava* is found only in bamboo habitats in southwestern Amazonia, and is thus considered to be a bamboo forest specialist (Isler et al. 2007, Lebbin 2013, Guilherme 2016, Pedroza & Guilherme 2019). Although *H. peruviana* and *H. subflava* are not sister species (Tobias et al. 2008), they have highly similar territorial songs and apparently compete for access to space and resources in the sympatric zone (Tobias & Seddon 2009, Kirschel et al. 2019). While both species respond to the territorial song of its congener, the response of *H. subflava* tends to be relatively weak in comparison to that of *H. peruviana* (Tobias & Seddon 2009). This difference may contribute to the behavioral dominance of *H. peruviana* over *H. subflava* (Tobias & Seddon 2009).

In addition to agonistic behavior, variation in biometric traits may also favor the dominance of one species over another (Morse 1974, Chappell 1978, Robinson & Terborgh 1995). Larger species tend to occupy larger spaces and consume greater amounts of resources in comparison with smaller species (Robinson & Terborgh 1995). In Amazonia, sympatric congener bird species (sister groups or not) tend to have non-overlapping territories, and typically, the dominant species is the largest in body size (Robinson & Terborgh 1995). Morphological differences may also be found between the males and females of a species, a phenomenon known as sexual dimorphism (Møller & Pomiankowski 1993). In birds, this difference is primarily found in the plumage and body dimensions, although males and females may also vary in size and body mass (Berns & Adams 2010, Chaves & Alves 2013, Maccarone & Brzorad 2016).

Receipt 19 July 2019 · First 25 September decision 2019 · Acceptance 6 November 2019 · Online publication

Communicated by Marcos Raposo & Rafael Rueda-Hernández © Neotropical Ornithological Society

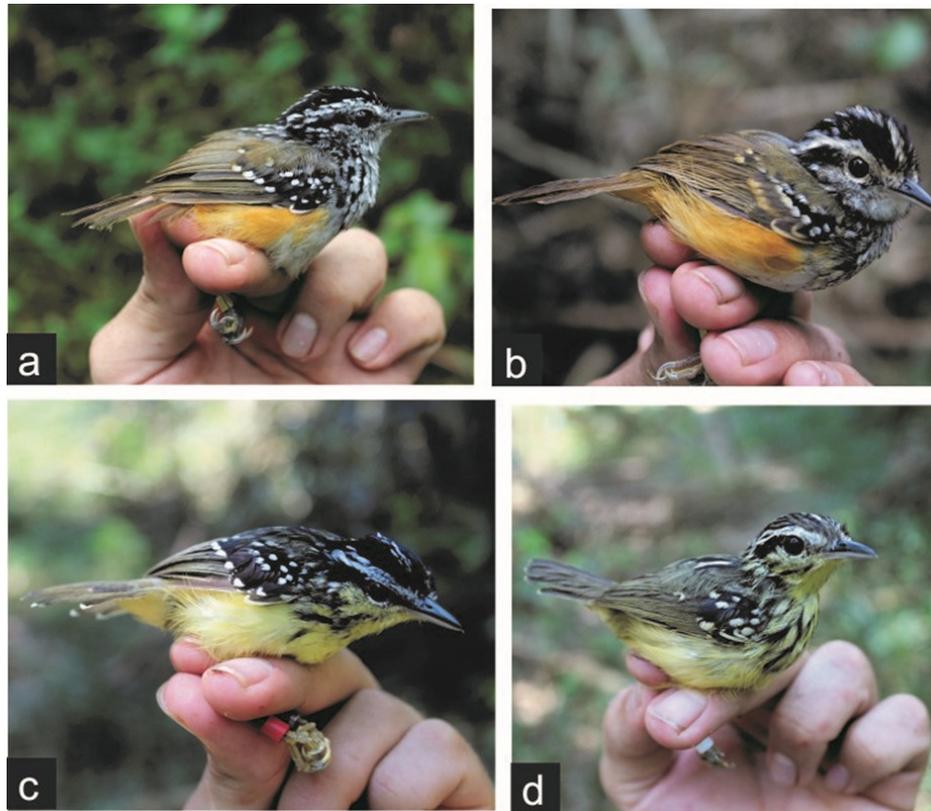


Figure 1. Comparison of male (left) and female (right) *Hypocnemis peruviana* (a, b) and *Hypocnemis subflava* (c, d) individuals.

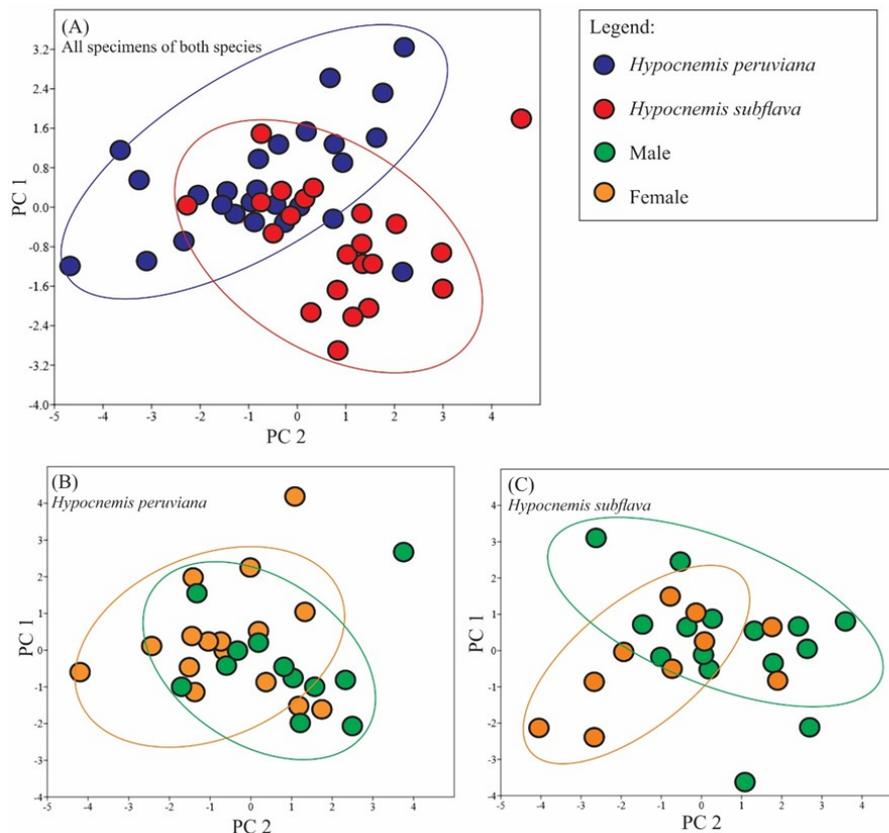


Figure 2. Plot of the Principal Components Analysis (PCA) of the biometry of the (A) Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and the Yellow-breasted Warbling-Antbird (*H. subflava*). (B) Male and female *H. peruviana*, (C) Male and female *H. subflava*. The percentage variance, eigenvalues, and loadings are shown in Table 1.

Aggressive responses to the territorial songs of *H. subflava* and the apparent biometric differences between the two species may favor the dominance of *H. peruviana* over *H. subflava* (Tobias & Seddon 2009). However, while Tobias & Seddon (2009) referred to biometric differences between these two species, they did not provide any empirical data or

analyses. In fact, the few biometric data available on the genus *Hypocnemis* referred to *H. hypoxantha* and the *H. cantator* complex (Graves & Zuzy 1990, Silva et al. 1990, Dunning 2008). Isler et al. (2007) divided the *H. cantator* complex into six distinct species, based on the vocalizations and geographic distribution. With this arrangement

Table 1. Results of the Principal Components Analysis (PCA), showing the percentage variance, eigenvalues, and loadings for axes PC1 and PC2 of the biometric measurements of *H. peruviana* and *H. subflava* and for the comparison of the sexes of the two species. The most relevant loadings are highlighted in bold type.

PC	<i>H. peruviana</i> and <i>H. subflava</i>		Male and female <i>H. peruviana</i>		Male and female <i>H. subflava</i>	
	PC1	PC2	PC1	PC2	PC1	PC2
Variance (%)	31.18	15.41	32.04	23.08	34.03	20
Eigenvalue	3.12	1.54	3.20	2.31	3.40	1.96
Biometric variable	Loading		Loading		Loading	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Beak height	0.19	0.57	0.06	0.53	0.30	0.16
Beak width	0.42	0.16	0.43	0.24	0.36	0.31
Wing	0.36	-0.31	0.38	0.31	0.34	0.30
Retrices	0.37	0.00	0.30	0.02	0.33	0.38
Tarsus length	-0.14	0.49	0.10	0.41	0.00	0.17
Beak length	0.47	-0.13	0.51	0.03	0.43	0.23
Tarsus width	0.05	0.51	0.42	0.27	0.30	0.04
Head	0.41	0.02	0.29	0.32	0.40	0.24
Total length	0.30	0.01	0.17	0.39	0.21	0.53
Body mass	-0.16	-0.17	0.05	0.25	0.24	0.44

accepted, the biometrics of each of the new species, including *H. peruviana* and *H. subflava*, have never been studied in detail. Given this, we investigated the degree of biometric differentiation (morphometry and body mass) between *H. peruviana* and *H. subflava*, in order to provide an empirical database for the evaluation of the proposed dominance relationship between the two species. We also verified whether differences in the same parameters are found in the males and females of the two species.

METHODS

We collected biometric data on *H. peruviana* and *H. subflava* from four localities in the eastern Acre state, northwestern Brazil (region of sympatry). These sites were the Zoobotanical Park (9°57'4.4"S, 67°52'26.3"W), the Catuaba Experimental Farm (10°4'12"S, 67°36'43.3"W), the Humaitá Forest Reserve (9°45'18.3"S, 67°40'14.1"W), and the Afluente Glebe (8°39'50"S, 69°37'30.8"W). We measured a total of 52 adult individuals, 24 *H. peruviana* (14 males and 10 females) and 28 *H. subflava* (17 males and 11 females; Figure 1). We recorded the following biometric variables: beak height (from the base of the exposed culmen, just in front of the feathering); beak length (from the angle at the front of the skull to the tip of the beak); beak width (laterally, from the edge of the feathering); tarsus length and width (length: from the joint between tarsus and toes to the intertarsal joint; width: taken from the middle of the tarsus); flattened wing chord length (from the carpal joint to the tip of the longest primary); rectrix length (from between the two innermost retrices, where their bases emerge from the skin, to the tip of the longest tail feather); head size (head plus beak); total length (with the live bird laid on its back on a ruler, measurement taken from the tip of the beak to the tip of the retrices), and body mass. Measurements were taken using a digital caliper (precision 0.01 mm), ruler (for full length only), and digital

balance (body mass, precision of 0.1 g), following the protocol of Proctor & Lynch (1993).

We ran a Principal Components Analysis (PCA) to summarize the variation in the biometric patterns of *H. peruviana* and *H. subflava*, as well as between the sexes of the two species. The PCA was applied to the correlation matrix to normalize the variables, which were divided by their standard deviations. We used a PERMANOVA, with adjustment for Euclidean distance, to test whether the raw variables differ between the species or the sexes of each species (Anderson 2005). We ran these analyses separately, first testing the biometric variation between species and then that between the males and females of each species. We applied a t-test to determine the degree of difference in each variable between *H. peruviana* and *H. subflava* and between the sexes of the two species. We assessed the normality of the residuals using the Shapiro-Wilk test, and the homoscedasticity of the variances with Levene's test. We ran the analyses in Past 3.14 (Hammer et al. 2001).

RESULTS

The PCA using the entire sample of *H. peruviana* and *H. subflava* revealed that 31.18% of the variation in the data was explained by axis 1 (PC1) and 15.41% by axis 2 (PC2), with a total of 46.59% of the variation being accounted for by the first two axes (Table 1, Figure 2). On axis 1, beak width, beak length, and head length had the highest loadings while on axis 2 beak height and the length and width of the tarsus had the highest loading values (Table 1). The results of PERMANOVA indicated that both species have significant morphological differences ($F = 5.25$, $P = 0.004$).

The PCA using only *H. peruviana* samples revealed that axis 1 (PC1) explained 32.04% of the variation and axis 2 (PC2) 23.08% of it, with a total of 55.12% of the variation being accounted for by these two axes (Table 1, Figure 2). On

Table 2. Mean, standard deviation (SD), and values of *t* and *p* for the biometric variables of Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*) specimens, captured in eastern Acre state, Brazil. Significant differences are highlighted in bold type, and the highest mean is indicated by an asterisk (*).

Species	Variable (Mean ± SD)	<i>t</i>	<i>p</i>
	<i>Beak height (mm)</i>		
<i>Hypocnemis peruviana</i>	4.05 ± 0.30	0.91	0.37
<i>Hypocnemis subflava</i>	4.15 ± 0.40		
	<i>Beak width (mm)</i>		
<i>Hypocnemis peruviana</i>	5.18 ± 0.61*	2.13	0.04
<i>Hypocnemis subflava</i>	4.80 ± 0.59		
	<i>Wing (mm)</i>		
<i>Hypocnemis peruviana</i>	54.10 ± 2.64	1.32	0.19
<i>Hypocnemis subflava</i>	53.14 ± 2.30		
	<i>Retrices (mm)</i>		
<i>Hypocnemis peruviana</i>	39.76 ± 2.99*	2.41	0.02
<i>Hypocnemis subflava</i>	36.54 ± 5.44		
	<i>Tarsus length (mm)</i>		
<i>Hypocnemis peruviana</i>	20.48 ± 1.48	3.92	< 0.01
<i>Hypocnemis subflava</i>	22.07 ± 1.26*		
	<i>Beak length (mm)</i>		
<i>Hypocnemis peruviana</i>	15.41 ± 1.74*	2.13	0.04
<i>Hypocnemis subflava</i>	14.45 ± 1.26		
	<i>Tarsus width (mm)</i>		
<i>Hypocnemis peruviana</i>	1.42 ± 0.30	3.20	< 0.01
<i>Hypocnemis subflava</i>	2.53 ± 1.56*		
	<i>Head (mm)</i>		
<i>Hypocnemis peruviana</i>	33.70 ± 1.09	1.82	0.07
<i>Hypocnemis subflava</i>	32.63 ± 2.51		
	<i>Total length (cm)</i>		
<i>Hypocnemis peruviana</i>	12.17 ± 0.70*	3.15	< 0.01
<i>Hypocnemis subflava</i>	11.63 ± 0.45		
	<i>Body mass (g)</i>		
<i>Hypocnemis peruviana</i>	12.75 ± 1.04	0.08	0.94
<i>Hypocnemis subflava</i>	12.72 ± 0.93		

axis 1, beak width and length and tarsus width had the highest loadings whereas on axis 2 beak height and the length of the tarsus had the highest loading values (Table 1). The results of PERMANOVA indicated no systematic sexual dimorphism in *H. peruviana* ($F = 1.43$, $P = 0.21$).

In the case of *H. subflava*, the results of the within-species PCA indicated that 34.03% of the variation between the sexes was explained by axis 1 (PC1) and 20% was explained by axis 2 (PC2), with a total of 54.03% of the variation being explained by the first two axes (Table 1, Figure 1). On axis 1, the lengths of the beak and head had the highest loading values, while on axis 2 only the total length had a meaningful loading value (Table 1). Like before, we found no systematic morphological differences between male and female *H. subflava* (PERMANOVA, $F = 2.65$, $P = 0.07$).

The *t* test indicated significant differences between *H. peruviana* and *H. subflava* in six biometric variables (Table 2), with *H. peruviana* presenting larger beaks (length and width), longer retrices, and higher values of body length, whereas only the tarsus (length and width) of *H. subflava* were longer than those of *H. peruviana*. Significant differences were recorded in four biometric variables between male and female individuals of *H. peruviana* (beak height, tarsus, head, and total length) with all males having higher values for these variables than the females (Table 3). In *H. subflava*, only the mean beak height of the males was larger than that of the females (Table 3).

DISCUSSION

We confirmed the existence of significant biometric differences between *H. peruviana* and *H. subflava*, with *H. peruviana* being slightly larger than *H. subflava*, in general. Our results indicate that the length and breadth of the beak represent one of the main biometric differences found among the species. The retrices are also larger, on average, in *H. peruviana* (Table 2). As both the beak and the retrices are larger in *H. peruviana*, it seems reasonable to conclude that this species is larger overall (total length) than *H. subflava*. Despite these biometric differences between the two taxa, they may be too subtle to allow the differentiation of the two species in the field. As their vocalizations are also very similar (Tobias & Seddon 2009), the only reliable way to differentiate these two species in the sympatric zone is through the differences in their plumage (Figure 2) and their occupied habitat, whether they are present in bamboo habitats or not (Pedroza & Guilherme 2019). Similar results were obtained regarding sexual dimorphism. Once again, as the males and females of neither species can be differentiated based on their biometric parameters, they can only be identified based on subtle differences in their plumage (Figure 2).

These biometric differences between the species, together with the aggressive response of *H. peruviana* to the territorial song of *H. subflava*, as verified by Tobias & Seddon

Table 3. Mean, standard deviation (SD) and the values of *t* and *p* for the biometric variables of male and female Peruvian Warbling-Antbird (*Hypocnemis peruviana*) and Yellow-breasted Warbling-Antbird (*Hypocnemis subflava*) specimens, captured in eastern Acre state, Brazil. Significant differences are highlighted in bold type, and the highest mean is indicated by an asterisk (*).

<i>Hypocnemis peruviana</i>	Variable (Mean ± SD)	<i>t</i>	<i>p</i>	<i>Hypocnemis subflava</i>	Variable (Mean ± SD)	<i>t</i>	<i>p</i>
	<i>Beak height (mm)</i>				<i>Beak height (mm)</i>		
Male	4.17 ± 0.31*	2.22	0.04	Male	4.31 ± 0.35*	2.67	0.01
Female	3.90 ± 0.22			Female	3.92 ± 0.38		
	<i>Beak width (mm)</i>				<i>Beak width (mm)</i>		
Male	5.23 ± 0.70	0.44	0.66	Male	4.90 ± 0.67	1.02	0.32
Female	5.10 ± 0.50			Female	4.65 ± 0.44		
	<i>Wing (cm)</i>				<i>Wing (cm)</i>		
Male	53.92 ± 2.81	0.34	0.74	Male	53.82 ± 2.21	1.93	0.07
Female	54.33 ± 2.55			Female	52.11 ± 2.11		
	<i>Retrices (mm)</i>				<i>Retrices (mm)</i>		
Male	40.25 ± 3.02	0.86	0.40	Male	38.1 ± 4.17	1.84	0.08
Female	39.11 ± 3.02			Female	34.2 ± 6.48		
	<i>Tarsus (mm)</i>				<i>Tarsus (mm)</i>		
Male	21.23 ± 1.22*	3.30	< 0.01	Male	22.17 ± 1.13	0.50	0.62
Female	19.47 ± 1.19			Female	21.91 ± 1.47		
	<i>Beak length (mm)</i>				<i>Beak length (mm)</i>		
Male	15.32 ± 1.87	0.24	0.81	Male	14.76 ± 1.35	1.49	0.15
Female	15.51 ± 1.67			Female	14.00 ± 1.05		
	<i>Tarsus length (mm)</i>				<i>Tarsus length (mm)</i>		
Male	1.51 ± 0.32	1.70	0.11	Male	2.43 ± 1.53	0.38	0.70
Female	1.30 ± 0.25			Female	2.68 ± 1.68		
	<i>Head (mm)</i>				<i>Head (mm)</i>		
Male	34.13 ± 1.13*	2.26	0.04	Male	32.99 ± 3.00	0.88	0.38
Female	33.14 ± 0.76			Female	32.08 ± 1.52		
	<i>Total length (mm)</i>				<i>Total length (mm)</i>		
Male	12.43 ± 0.81*	2.15	0.05	Male	11.73 ± 0.46	1.41	0.17
Female	11.82 ± 0.31			Female	11.48 ± 0.41		
	<i>Body mass (g)</i>				<i>Body mass (g)</i>		
Male	12.44 ± 1.02	1.61	0.12	Male	12.69 ± 1.11	0.82	0.48
Female	12.90 ± 0.72			Female	12.96 ± 0.60		

(2009), reinforce the conclusion that *H. peruviana* is dominant over *H. subflava* in the areas of Amazonia in which these two species are found in sympatry. In addition to the biometric differences and the agonistic behavior observed in one of the species, the dominant taxon is also expected to have a higher population density (Rajpar & Zakaria 2011, Bupalov & Belyaev 2018). Given this, we would recommend a more systematic investigation of this parameter (population density) in the areas where the two species occur in sympatry.

One other factor that supports the classification of the two species as dominant-subordinate is their foraging specializations (Freshwater et al. 2014), with the subordinate species typically foraging differently than its dominant conge-

ner. *Hypocnemis subflava* is found exclusively in bamboo habitats (Isler et al. 2007, Lebbin 2013, Guilherme 2016, Pedroza & Guilherme 2019), in contrast to *H. peruviana*, which is found in other types of environments (Isler et al. 2007, Tobias & Seddon 2009, Guilherme 2016). Specialization of *H. subflava* towards bamboo habitats further reinforces the conclusion that this species may be the subordinate member of the pair.

We found no sexual dimorphism in the biometric traits of neither *H. peruviana* or *H. subflava* in our multivariate analysis. This suggests that the biometric traits of males and females of these species do not affect the behavioral patterns of dominance between the sexes. However, the results of the t-test indicate that the *H. peruviana* male is significantly

larger than the female in a number of traits, although a significant difference was found for *H. subflava* only in beak height. (Table 3). A similar situation was recorded in an endemic thamnophilid from the Atlantic forest in Brazil, the Restinga Antwren (*Formicivora littoralis*); for this species, some biometric measurements of the male, such as those of the beak, were found larger than those of the female (Chaves & Alves 2013). Differences between the sexes in some biometric traits may minimize the competition for resources between males and females (Selander 1966, Holmes 1986), given that distinct traits may support the exploitation of different types of resources, thus minimizing the feeding competition between the sexes (Selander 1966, Holmes 1986).

Differences in biometric traits are not in themselves sufficient evidence to confirm the dominance of one of the sexes in *H. peruviana* and *H. subflava*, considering the need to confirm agonistic behavior and distinct patterns of foraging behavior between males and females, which are consistent with the dominance of one sex over the other (Holmes 1986, Verbeek et al. 1996). In addition, there is no evidence of any sexual dimorphism in the territorial song in neither of the species, given that the males and females of both species have highly similar territorial songs (Seddon & Tobias 2006). This evidence further reinforces the conclusion that there is no dominance of one sex over the other in *H. peruviana* and *H. subflava*. Alternatively, slightly larger males are expected if males are under sexual selection.

Overall, we can conclude that the biometric differences found between *H. peruviana* and *H. subflava* may contribute to the dominance of one species over the other. While some biometric traits vary significantly between the sexes in both species, we do not believe that the differences are enough to ensure the behavioral dominance of one of the sexes over the other in both species. Even so, these biometric differences may contribute to reducing resource competition between the sexes.

ACKNOWLEDGMENTS

We are grateful to the Masters Program in Ecology, the Management of Natural Resources of the Federal University of Acre, and the National Center for Research and Conservation of Wild Birds (CEMAVE/ICMBio). We would also like to thank the researchers David Guimarães, Jonatas Lima, and Vanessa de Souza for capturing some of the specimens analyzed, and the biologist Richarlly Costa for help and suggestions with the statistical analyses.

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