

1 **Bird songs on the shelf: assessing vocal activity and output using data hidden in**

2 **sound archives**

3

4 Short title: Bird songs on the shelf.

5

6 Oscar Laverde-R.<sup>a,b</sup>, Paula Caycedo-Rosales<sup>c</sup>, Paulo-C. Pulgarín-R.<sup>a</sup> & Carlos Daniel

7 Cadena<sup>a</sup>

8

9 <sup>a</sup> Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias

10 Biológicas, Universidad de los Andes.

11

12 <sup>b</sup> Current address: Unidad de Ecología y Sistemática (UNESIS), Departamento de

13 Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Bogotá D. C.

14

15 <sup>c</sup> Fundación Biodiversa Colombia. Bogotá, D. C.

16

17 Address correspondence to Oscar Laverde-R.

18

19 E-mail: [laverdeo@javeriana.edu.co](mailto:laverdeo@javeriana.edu.co)

20

21

22

23

24 **Abstract**

25 Understanding how often do animals emit communication signals is of critical  
26 importance to address a variety of research questions in behavioral ecology and sexual  
27 selection. However, information on vocal output, a central component of investment in  
28 signaling, is lacking for most species employing acoustic communication. Because this  
29 lack of information is partly due to logistical and methodological difficulties in  
30 monitoring animal signaling over time, developing new approaches to quantify vocal  
31 output is of special importance. We asked whether the number of recordings of avian  
32 vocalizations in sound archives and the times when such recordings were obtained reflect  
33 estimates of vocal output and temporal patterns of vocal activity obtained through  
34 systematic monitoring of wild bird populations in tropical forest sites. Based on a sample  
35 of 43 montane forest species, we found significant relationships between the number of  
36 recordings of species detected through continuous monitoring over several months and  
37 the number of recordings archived in sound collections, especially when accounting for  
38 the area of distribution of each species. In addition, daily activity patterns based on data  
39 collected through continuous monitoring over several days did not differ from those  
40 based on recordings archived in sound collections in 12 of 15 species of lowland forest  
41 birds. Annual patterns in vocal activity of two species estimated based on recordings in  
42 collections closely resembled previously published patterns. We conclude that recordings  
43 in sound collections contain valuable yet previously unappreciated information about the  
44 vocal output and temporal patterns in vocal activity of birds. This opens the possibility of  
45 using sound collections to assess vocal output and to consider it as a variable of interest  
46 in studies on the ecology and evolution of birds and other animals that use acoustic

47 signals for communication. We encourage field workers to keep the ears wide open, and  
48 the recorders wide ready to record.

49

## 50 **INTRODUCTION**

51 Understanding how often do animals emit communication signals over various time  
52 frames is of critical importance to address a variety of research questions in behavioral  
53 and evolutionary biology. In particular, birdsong is a model system for the study of  
54 animal communication and sexual selection (Read & Weary 1992; Slater 2003). Mate  
55 choice by females in many bird species is influenced by male singing behavior and song  
56 structure, with different attributes of songs being targets of sexual selection (Cardoso &  
57 Hu 2011). For example, because traits such as song length, consistency, rate, repertoire  
58 size, syllable variety, and trill syntax are attributes commonly selected by females, they  
59 are often the focus of behavioral and evolutionary studies on acoustic signals (Arvidsson  
60 & Neergaard 1991; Podos 1997; Gil & Slater 2000; Gil & Gahr 2002; Ballentine 2004;  
61 Botero *et al.* 2009; Cardoso & Hu 2011; Woodgate *et al.* 2012; Derryberry *et al.* 2012).  
62 Because singing is time-consuming, energetically costly, and may entail other costs (e.g.,  
63 increased predation), studies on acoustic communication and sexual selection would  
64 benefit from understanding the costs that birds accrue when singing over longer time  
65 frames (e.g., complete breeding seasons, Krams 2001; Gil and Gahr 2002; Shutler 2011).  
66 Although some properties of single vocalizations are related to song elaboration or  
67 complexity and may thus represent partially adequate proxies of some of the costs  
68 involved in singing, they cannot fully capture the variation existing among individuals  
69 and species in singing strategies and their associated costs. What is more costly: to emit a

70 highly elaborate song sporadically, or to emit a simple song constantly? One cannot begin  
71 to address questions like this one without basic information about when and how often do  
72 birds sing.

73

74 Patterns of circadian variation in the vocal activity of birds are not well-known, except  
75 for the fact that, generally, birds sing more at dawn (and sometimes at dusk) than at other  
76 times of the day (Aide *et al.* 2013). Daily patterns in the vocal activity of tropical birds  
77 have not been studied in detail, except for a few studies finding that canopy birds begin  
78 singing earlier than understory birds during dawn choruses (Berg *et al.* 2006), or that  
79 vocal activity in understory birds declines markedly one hour after sunrise while vocal  
80 activity in canopy birds tends to increase 1-2 hours after dawn and then declines (Blake  
81 1992). Nonetheless, some tropical birds are more active at different times of the day (e.g.,  
82 at around noon in some woodcreepers, Antunes 2008). Beyond these general  
83 observations, however, quantitative data on daily patterns in avian vocal activity are  
84 notoriously scarce, especially for tropical species.

85

86 It is generally assumed that most birds from the temperate zone exhibit marked seasonal  
87 patterns of vocal activity over the year, but this is often thought not to be the case for  
88 species from tropical, more stable environments (Stutchbury & Morton 2001). However,  
89 many tropical species show breeding seasonality in response to pulses in resource  
90 abundance and climate (Wikelski *et al.* 2000), and because reproduction correlates with  
91 increased vocal activity, one should expect seasonal variation in singing behavior. Some  
92 species sing throughout the year (e.g., Koloff & Mennill, 2012; Topp & Mennill, 2008),

93 whereas others show markedly seasonal patterns of vocal activity correlated with  
94 reproduction (e.g., Negret et al. 2015; Stutchbury & Morton 2001). Even in species that  
95 sing constantly during the year, vocal activity may vary seasonally, increasing during the  
96 breeding period (e.g., Koloff & Mennill 2012; Chiver et al. 2015).

97

98 In sum, it appears clear that the singing behavior of birds needs to be described in more  
99 detail, especially in the tropics. Because this would require direct study of the behavior of  
100 individual species over long periods of time (minimally one year) and in several places,  
101 which would be highly time-consuming and rather expensive, developing alternative  
102 means to study temporal patterns in vocal activity and vocal output (i.e., how often do  
103 birds sing) would be highly desirable. Based on the idea that information associated with  
104 museum or herbarium specimens has been used to characterize the annual cycles of  
105 organisms (e.g., flowering or fruiting phenology in plants; Borchert 1996; Boulter et al.  
106 2006; Zalamea et al. 2011), here we explore the possibility of using information archived  
107 in sound collections to describe patterns of variation in avian vocal activity and vocal  
108 output.

109

110 Sound archives are collections of field recordings of animal vocalizations focusing  
111 mainly on birds, frogs, fishes, mammals and insects. For instance, the Colección de  
112 Sonidos Animales (CSA) of the Instituto Alexander von Humboldt, Colombia, created 20  
113 years ago, holds around 20,000 bird recordings from this country. The Macaulay Library  
114 of Natural Sounds (MLS) at Cornell University holds around 175,000 audio recordings of  
115 more than 7,500 bird species from around the world. Xeno-canto (XC;

116 canto.org/), a website where field researchers and bird watchers share recordings of  
117 sounds of wild birds from all over the world, has accumulated ca. 315,000 recordings of  
118 more than 9,600 bird species since it was launched in May 2005. Recordings deposited in  
119 these and other sound collections have primarily been used for species identification,  
120 general bioacoustic analyses, and as records for distributional and biogeographical  
121 studies; we propose that these archives might also offer ample yet unexplored  
122 information about vocal output and temporal patterns of vocal activity.

123

124 Because recordists rely on the vocal activity of birds to record songs and calls, one may  
125 expect the number of recordings archived in sound collections to reflect how often do  
126 birds sing. For instance, the Gray-breasted Wood-Wren (*Henicorhina leucophrys*) is a  
127 common Neotropical bird that sings throughout the year; accordingly, sound collections  
128 contain a large number of recordings of this species (380 in CSA, 182 in MLS and 288 in  
129 XC as of July 2016; Table S1). The Spangled Cotinga (*Cotinga cayana*), in contrast, is a  
130 widespread species that apparently does not use acoustic signals as its main  
131 communication channel; not a single recording of it is to be found in CSA, MLS or XC.

132 If this pattern is consistent (i.e. that species investing more heavily in vocal  
133 communication are better represented in sound archives), then one may potentially use  
134 the number of recordings in sound collections as an index of vocal output. In addition,  
135 because recordists rely on temporal patterns of vocal activity to record birds, then one  
136 may further expect that information on the date and time when recordings in sound  
137 collections were obtained would give insights about annual and daily patterns of vocal  
138 activity. However, to make valid inferences about vocal output and temporal patterns in

139 vocal activity based on archived recordings, one would first need to validate this  
140 approach with data on vocal activity measured directly in the field.  
141  
142 We asked whether the number of recordings in sound archives and when such recordings  
143 were obtained reflect estimates of vocal output and temporal patterns of vocal activity  
144 obtained through systematic monitoring of wild bird populations. Specifically, we  
145 evaluated the hypothesis that one can obtain adequate estimates of vocal output and  
146 temporal patterns in vocal activity from sound archives by testing the predictions that (1)  
147 there is a positive relation between the number of recordings of each species deposited in  
148 archives and the number of vocalizations detected via direct field monitoring in three  
149 contrasting tropical forest sites, and (2) that there are no differences in the temporal  
150 distributions of recordings available in sound archives and of recordings obtained through  
151 continuous monitoring. Our results suggest that sound recordings in collections may in  
152 fact be used to assess vocal output and to describe temporal patterns of variation in the  
153 singing activity of birds, and potentially of other animals, for various types of studies.

154

## 155 **MATERIAL AND METHODS**

156 We evaluated whether recordings in sound archives reflect vocal output and temporal  
157 patterns in vocal activity described on the basis of systematic monitoring of bird  
158 populations using sound recordings obtained with autonomous recording units (ARUs,  
159 Rempel et al. 2013). To accomplish this, we first used ARUs (Wildlife Acoustics  
160 SongMeter II) to (1) measure vocal output over a period of seven months (including dry  
161 and wet seasons) in a tropical montane forest and (2) to quantify daily patterns in vocal

162 activity in two tropical lowland humid forests. We then compared our data from these  
163 field sites with information extracted from sound archives.

164

### 165 *Measuring vocal output*

166 We studied vocal output of avian species over several months in a tropical montane forest  
167 in Chingaza National Park, eastern Andes of Colombia. Chingaza is located ca. 40 km  
168 east of the city of Bogotá in the departments of Cundinamarca and Meta. Approximately  
169 190 bird species in 40 families occur in the park (Vargas & Pedraza 2004). The region  
170 has an average annual precipitation of 1800 mm, with two distinct peaks. The dry season  
171 extends from November to March with minimum rainfall in January and February, and  
172 the wet season extends from April to October with maximum rainfall in June and July  
173 (Vargas & Pedraza 2004).

174

175 We sampled avian vocal activity in the Palacio sector of Chingaza National Park (4°41'  
176 N, 73°50' W) in six different locations (Table 1). ARUs were located in forests between  
177 2950 and 3170 m elevation and placed more than 500 m away from each other to avoid  
178 recording the same individuals in more than one unit. Each ARU was programmed to  
179 record for three minutes every 30 minutes. We sampled vocal activity over several  
180 months in 2013 (Table 1): February (four ARUs), April (three ARUs), May (four ARUs),  
181 July (two ARUs), and August (two ARUs). We listened to recordings obtained from 5:30  
182 am to 12:00 m (vocal activity decreasead markedly later in the day) and identified  
183 vocalizing species (90% of avian vocalizations detected were identified to species). For  
184 each identified sound we registered the species, type of vocalization (song or call), date,



185 and time of day. We included in analyses 43 species with more than two recordings (i.e.,  
186 we excluded nine species recorded only once or twice).

187

188 We set to test whether the number of recordings of a given species deposited in sound  
189 archives is a valid proxy of its vocal output (i.e., how often does it sing). Thus, for the 43  
190 species detected in field recordings in Chingaza and included in the analyses, we tallied  
191 the number of recordings archived in three different sound archives: CSA, MLS and XC.  
192 CSA holds about 20,000 recordings from Colombia, with special focus in the Andes, the  
193 Amazon Basin and the Caribbean Region. MLS is one of the largest collections of bird  
194 recordings in the world, with material from the Neotropics mainly from Peru (ca. 13,000),  
195 Brazil (ca. 10,000), Venezuela (ca. 8,500), and Ecuador (ca. 6,000); Colombia is not as  
196 well represented in this collection, with only ca. 1000 recordings. XC is a web-based,  
197 rapidly growing archive with ca. 120,000 recordings from South America; in the region,  
198 the best represented countries in terms of number of recordings are Brazil (ca. 25,000),  
199 Colombia (ca. 13,000), Peru (ca. 12,000), and Ecuador (ca. 9,000).

200

201 Distributional range size likely affects the number of recordings of each species in  
202 archives (i.e., one expects more available recordings of more widespread species).  
203 Therefore, we controlled for the effect of area of the distributional range (see below) on  
204 number of recordings for each species using Nature Serve range maps (Ridgely *et al.*  
205 2003). Because the abundance of birds may also affect the number of recordings in  
206 archives, we also sought to correct for abundance using bird-count data collected over ten

207 months in Finca Cárpatos, Chingaza (2800-3100 m; 4°42' N, 73°51' W), a location very  
208 close to our study site in Palacio (Stiles and Roselli 1998; see below).

209

210 *Quantifying temporal activity patterns*

211 We studied vocal activity along the day for avian species assemblages in two lowland  
212 forest sites. First, Barbacoas (6°41' N, 74°21' W) is a humid lowland forest located in  
213 Antioquia Department, in the middle Magdalena Valley of Colombia at 300 m elevation.  
214 Pastures for cattle dominate the area, but some fragments of primary forest remain.  
215 Approximately 250 bird species in 53 families have been recorded in the area (O.  
216 Laverde-R. et al., unpubl. data). The region has an average annual precipitation of 2200  
217 mm, with two distinct peaks. The dry season extends from December to March, with  
218 minimum rainfall in January, and the wet season extends from April to October with  
219 maximum rainfall in September and October (IDEAM,  
220 <http://bart.ideam.gov.co/cliciu/barran/precipitacion.htm>). Second, Bahía Málaga (3°58' N,  
221 77°19' W) is located on the Colombian Pacific coast in the Chocó biogeographic region,  
222 in Chocó Department. There are no published avian inventories of the area, but more than  
223 300 species are expected to occur in the region (Hilty & Brown 1986). The region has an  
224 average annual precipitation of 7300 mm, with two distinct peaks. The region is wet year-  
225 round, but rainfall is lower from January to February, and the wet season extends from  
226 March to November with maximum rainfall in September and October (IDEAM,  
227 <http://bart.ideam.gov.co/cliciu/buena/precipitacion.htm>).  
228

229 To sample avian vocal activity during the day, we set two ARUs in Barbacoas for 19 days  
230 (18 December 2012 to 5 January 2013) and two ARUs in Bahía Málaga for five days (2  
231 July 2014 to 6 July 2014). ARUs were placed in tall primary forest and were programmed  
232 to record for 3 minutes every 30 minutes, from 05:30 h to 18:00 h. We listened to  
233 recordings and identified vocalizing species; for each identified sound we registered the  
234 species, type of vocalization (song or call), and time of day. We selected the 15 most  
235 frequently recorded species (i.e., those with at least 30 recordings in ARUs) for analyses  
236 of variation in vocal activity along the day (Table 2). For the above 15 lowland species,  
237 we extracted information on the time of day associated with all the recordings deposited  
238 in XC. We analyzed all archived recordings of these species (i.e., not exclusively those  
239 from our study region or from Colombia) to ensure sufficient sample sizes were available  
240 for analyses.

241

242 We also explored whether annual patterns of vocal activity may also be studied using  
243 recordings deposited in sound collections. We selected two species known to exhibit  
244 seasonal patterns of vocal activity along the year and which are well represented in sound  
245 collections: the Clay-colored Thrush (*Turdus grayi*) and the Great Tinamou (*Tinamus*  
246 *major*). The Clay-colored Thrush exhibits a marked peak in vocal activity in the first part  
247 of the year (March-April; Figure 6.1 in Stutchbury & Morton 2001), whereas the vocal  
248 activity of tinamous is known to vary seasonally, with peaks especially in the dry season  
249 (Lancaster 1964; Negret et al. 2015). Because Great Tinamou has a broad latitudinal  
250 distribution and precipitation regimes (hence likely breeding and vocal activity) differ  
251 between hemispheres, we analyzed data only from the Northern Hemisphere. We

252 obtained the dates of recordings for these two species in MLS and XC, grouped them by  
253 month, and examined whether annual patterns of activity estimated using the recordings  
254 in archives matched expected patterns given published data.

255

### 256 *Statistical analyses*

257 To evaluate the hypothesis that the information archived in sound collections can be used  
258 to estimate vocal output and temporal patterns in avian vocal activity we tested the  
259 predictions that (1) vocal output measured via continuous monitoring using ARUs  
260 correlates positively with the number of recordings in collections and (2) that the hourly  
261 distribution of recordings obtained via continuous monitoring does not differ from the  
262 hourly distribution of recordings available in collections. To evaluate our first prediction,  
263 we regressed the number of recordings in sound collections against the area of the  
264 geographic range of each species, and then regressed the residuals of this analysis on the  
265 total number of recordings counted in our field recordings. To evaluate the effect of  
266 abundance in the number of recordings in sound collections, we regressed the number of  
267 recordings in sound collections against the abundance of each species (Stiles & Rosselli  
268 1992), and then regressed the residuals of this analysis on the total number of recordings  
269 counted in our field recordings. Variables were log-transformed to meet the normality  
270 assumptions of linear models. We also ran phylogenetic generalized least-square models  
271 (PGLS) to account for phylogenetic effects using the caper package for R (Orme *et al.*  
272 2012) based on a comprehensive avian phylogeny (Jetz *et al.* 2012).

273

274 To examine our second prediction, we used circular statistics. First, we evaluated whether  
275 the data obtained from ARUs and from XS were uniformly distributed along the day  
276 using a non-parametric Rayleigh test of uniformity; second, we used the Watson-  
277 Williams test to evaluate the null hypothesis that the two daily activity patterns (i.e., those  
278 obtained from ARUs and XC) are not statistically different (Kovach 2011). We also used  
279 Rayleigh tests of uniformity to assess whether vocalizations of Clay-colored Robin and  
280 Great Tinamou are uniformly distributed along the year, and qualitatively compared the  
281 annual patterns for these species revealed by recordings in MLS and XC with published  
282 data.

283

## 284 **RESULTS**

### 285 *Vocal output*

286 We examined 607 three-minute recordings from our tropical montane forest site in  
287 Chingaza; in 237 of these, no avian vocalizations were detected. We detected a total of  
288 2192 vocalizations in 370 recordings obtained using ARUs (Table S1). Of this total, we  
289 identified 1522 vocalizations as songs (70%) and 433 as calls (20%); we were unable to  
290 identify 237 vocalizations (10%). Among the 1522 identified songs we detected 52  
291 species from 19 families; for subsequent analyses we focused on 43 species having more  
292 than three recordings of songs during our sampling period (total 1512 individual songs;  
293 Table S1). For the species detected in ARUs, we found a total of 1363 recordings of  
294 songs in CSA, 1892 in MLS, and 1651 in XC.

295

296 The number of recordings of each species recorded in ARUs and in each of the sound  
297 collections were significantly and positively related (Figs. 1a-c): CSA ( $p < 0.0001$ ,  $\beta = 0.63$ ,  
298  $R^2 = 0.32$ ), MLS ( $p = 0.040$ ,  $\beta = 0.27$ ,  $R^2 = 0.076$ ), XC ( $p < 0.0001$ ,  $\beta = 0.42$ ,  $R^2 = 0.36$ ).  
299 Analyses correcting for size of the distributional range of species based on residuals  
300 (Figure 1) also revealed significant relationships and the explanatory power of models  
301 was considerably larger than that of models based on raw data (Figs. 1d-f): CSA  
302 ( $p < 0.0001$ ,  $R^2 = 0.41$ ), MLS ( $p < 0.0001$ ,  $R^2 = 0.42$ ) and XC ( $p < 0.0001$ ,  $R^2 = 0.40$ ). Similar  
303 results were obtained in PGLS analyses: CSA ( $p < 0.0001$ ,  $\beta = 0.69$ ,  $R^2 = 0.36$ ), MLS  
304 ( $p = 0.002$ ,  $\beta = 0.36$ ,  $R^2 = 0.14$ ), XC ( $p < 0.0001$ ,  $\beta = 0.48$ ,  $R^2 = 0.43$ ), with the explanatory  
305 power of models increasing when we included area of distributional range as a covariate:  
306 CSA ( $p < 0.0001$ ,  $R^2 = 0.43$ ), MLS ( $p < 0.0001$ ,  $R^2 = 0.48$ ) and XC ( $p < 0.0001$ ,  $R^2 = 0.45$ ).  
307 Analyses correcting for abundance based on residuals did not improve the explanatory  
308 power of models CSA ( $p = 0.0003$ ,  $R^2 = 0.25$ ), MLS ( $p = 0.13$ ,  $R^2 = 0.03$ ) and XC  
309 ( $p = 0.0001$ ,  $R^2 = 0.29$ ) even when accounting for phylogeny; CSA ( $p = 0.07$ ,  $R^2 = 0.04$ ), MLS  
310 ( $p = 0.81$ ,  $R^2 = -0.02$ ), XC ( $p = 0.0001$ ,  $R^2 = 0.23$ ).

311

### 312 *Vocal activity*

313 We examined 708 and 697 three-minute recordings from Barbacoas and Bahía Málaga,  
314 respectively. Of these, 431 and 430 recordings, respectively, contained avian  
315 vocalizations, resulting in a total of 1144 individual detections of species. Vocalizations  
316 recorded in the field using ARUs and those available in XC were not uniformly  
317 distributed over the day in any of our study species (Table S2; Figure 2). In 12 out of 15  
318 species, the hourly distribution of vocalizations did not differ between data collected

319 using ARUs and recordings available in XC, suggesting that both sources reveal similar  
320 circadian patterns of activity (Table 3). In two species of pigeon (Pale-vented Pigeon,  
321 *Patagioenas cayennensis* and Scaled Pigeon, *P. speciosa*) and one toucan (Black-billed  
322 Toucan, *Ramphastos ambiguus*) daily activity patterns were significantly different  
323 between data sets. In the pigeons, our recordings obtained using ARUs showed two clear  
324 peaks in vocal activity: one in the early morning and a second one in the late afternoon  
325 (Figure S1). Information in the XC collection did not reveal the same pattern: the peak in  
326 the morning was also clear, but the peak in the afternoon was not as evident. ARUs  
327 detected a bimodal pattern with clear peaks in the early morning and late afternoon in the  
328 singing activity of the toucan, but XC recordings showed a single peak during the mid-  
329 morning.

330

331 Annual patterns of vocal activity assessed using recordings available in XC and MLS  
332 were significantly seasonal (i.e., not uniform over time) for the Great Tinamou (MLS,  $z=$   
333  $18.816$ ,  $p<0.0001$ ; XC,  $z= 3.056$ ,  $p=0.04$ ) and the Clay-colored Thrush (MLS,  $z= 36.186$ ,  
334  $p<0.0001$ , XC,  $z= 34.877$ ,  $p<0.0001$ ). The recordings in sound archives indicate that  
335 Great Tinamou sings mostly from January to May with a peak in singing in March; the  
336 Clay-colored Thrush sings mostly from January to June with a peak in singing in April.  
337 These annual patterns based on archived recordings were similar to those described  
338 previously in the literature for species in the tinamou family (Lancaster, 1964; Negret et  
339 al. 2015) and for the Clay-colored Thrush (Stutchbury & Morton 2001).

340

341 **DISCUSSION**

342 The energetic costs of singing and how these costs are related to song complexity or  
343 elaboration is matter of debate (Eberhardt 1994; Oberweger and Goller 2001; Ward 2004;  
344 Garamszegi et al. 2006; Hasselquist and Bensch 2008). Some studies indicate that  
345 complex songs are not necessarily more costly than simple songs (Oberweger and Goller  
346 2001), but others suggest that complex songs can indeed be especially costly (Garamszegi  
347 et al. 2006). Regardless of any potential costs associated to song complexity, it is clear  
348 that some birds vocalize more frequently than others, implying that vocal output is a  
349 crucial variable one must consider when characterizing the variation in energy investment  
350 in vocal communication existing among species. However, vocal output is rarely  
351 evaluated in studies examining the costs of communication signals because information  
352 on how often do birds sing over various temporal scales (e.g. times of the day, months in  
353 a year) is lacking for most species. We suggest that a possible way to remedy the lack of  
354 consideration of vocal output in many studies is to use information deposited in sound  
355 collections. Our study supported the hypothesis that one can obtain meaningful estimates  
356 of vocal output and temporal patterns in vocal activity of tropical birds from information  
357 available in sound archives. This overlooked source of information may represent a  
358 crucial resource for researchers in acoustic communication, sexual selection, and other  
359 aspects of avian biology.

360

361 First, we found that recordings in sound collections can be used as a relatively accurate  
362 proxy of vocal output because the number of recordings of 43 species obtained through  
363 continuous monitoring over several months in a tropical montane forest were  
364 significantly related to the number of recordings collected non-systematically by various



365 field workers over multiple years and deposited in sound collections; this relation was  
366 stronger when correcting the number of recordings in collections by the size of the  
367 distributional range of species but not when correcting by species abundance. Second, we  
368 found that in 12 out of 15 lowland species the similar daily patterns of vocal activity were  
369 detected using data from continuous monitoring and from sound collections. Third, for  
370 two species, circannual patterns in vocal activity determined using information in sound  
371 collections matched patterns documented in the literature based on systematic studies.  
372 Although these results encourage the use of information in sound archives to characterize  
373 vocal output and temporal patterns in vocal activity, our analyses also revealed some  
374 possible sources of bias that researchers must consider; we discuss caveats related to such  
375 biases below.

376

377 Our analyses suggest that the suitability of archived recordings to characterize vocal  
378 output may vary among collections depending on their geographic focus. For example,  
379 the relationship between recordings archived at the MLS (the collection with the lowest  
380 numbers of recordings from Colombia; ca. 1,000) and recordings we obtained through  
381 continuous monitoring was weak relative to relationships obtained using recordings  
382 archived in the XC and CSA collections, which have much larger numbers of recordings  
383 from Colombia (ca. 13,000 and 20,000, respectively). This effect may be due to regional  
384 variation in vocal activity or abundance of species in different sectors of their distribution  
385 ranges, or may reflect bias resulting from differences in recording intensity effort (i.e.,  
386 collections with fewer recordings may not adequately capture patterns in vocal output due  
387 to insufficient sampling). Accordingly, the data we collected in the field for this project

388 revealed the importance of sampling over long periods of time to adequately characterize  
389 the vocal output of species. We explored whether vocal output estimated using recordings  
390 made using ARUs over a few days reflected information in sound collections for the  
391 lowland species that we used to study daily patterns of vocal activity, finding this was not  
392 the case ( $F=0.04$ ,  $p=0.83$ ) even when controlling for the size of the distributional range of  
393 species ( $F=0.72$ ,  $p=0.5$ ). We attribute this to the fact that sound archives contain  
394 information obtained over long periods of time (i.e., multiple years including dry and wet  
395 seasons); this long-term sampling captures effects of seasonality in vocal activity that  
396 cannot possibly be revealed by data collected over short periods of time. Thus, we  
397 suggest that information in collections is not only useful to study vocal output, but also  
398 that it may provide more accurate characterizations of long-term vocal output than data  
399 collected by short-term studies.

400

401 Our work revealed that the number of recordings of species in collections is significantly  
402 related to the number of recordings of these species obtained at a single site via  
403 continuous monitoring; however, a considerable fraction of the variation in vocal output  
404 measured locally was unexplained by the frequency with which species were represented  
405 in collections. This is not unexpected given the nature of the data because collections  
406 contain information from many different sites obtained by dozens of field workers across  
407 time and space lacking the specific purpose of documenting vocal output. We explored  
408 whether aspects related to the singing behavior of species influenced the extent to which  
409 recordings in sound collections reflected vocal output estimated through continuous  
410 monitoring by examining the residuals of regression analyses relating the number of

411 recordings in collections to vocal output assessed using ARUs, after accounting for area  
412 of distribution. First, we hypothesized that information in collections should be a worse  
413 predictor of vocal output in species with more seasonal singing activity; however,  
414 residuals did not differ between vocally seasonal and non-seasonal species (CSA,  $t = -$   
415  $0.67$ ,  $p = 0.51$ ; MLS,  $t = -1.10$ ,  $p = 0.28$ ; XC,  $t = -1.03$ ,  $p = 0.30$ ). We considered a  
416 species as non-seasonal if it was present constantly in recordings throughout the five  
417 months sampled in Chingaza, and seasonal if it was only present in recordings from 1-3  
418 months (no species was present only in recordings from four months). Second, we also  
419 considered whether residual variation could be accounted for phylogenetic affinities;  
420 however residuals did not differ between non-passerines, suboscines and oscines (CSA,  
421  $F = 0.17$ ,  $p = 0.83$ ; MLS,  $t = -1.10$ ,  $p = 0.28$ ; XC,  $t = -1.03$ ,  $p = 0.30$ ).

422

423 It seemed reasonable to think that abundance influences the number of recordings in  
424 sound collections; however, we found that correcting for species abundance in our  
425 analyses did not improve the explanatory power of models relating data in sound  
426 collections to data obtained through continuous monitoring. This likely implies that birds  
427 are not recorded in proportion to their abundance by field workers contributing to sound  
428 collections; a similar conclusion has been reached for botanists collecting plant  
429 specimens for herbaria (ter Steege et al. 2011). Specifically, field workers are likely to  
430 only record few of the individuals of common species they detect, while they often try to  
431 record rare birds. That common birds may be under represented in collections while rare  
432 birds may be over represented relative to their abundance reflects not only that rarity is  
433 attractive to ornithologists, but also that most of the recordings archived in sound

434 collections were obtained for the purpose of documenting diversity (i.e., establishing the  
435 occurrence of rare species at sites, sampling geographical variation in vocalizations of  
436 widespread species) and not for the purpose of documenting the frequency with which  
437 species were encountered.

438

439 Although daily activity patterns based on data collected through continuous monitoring  
440 were similar to those based on recordings archived in sound collections in most of our  
441 study species, this was not the case in all of them. In particular, information in collections  
442 failed to reveal a peak in singing activity in the afternoon in two species of pigeon and a  
443 toucan. Recordists, like most birds, are more active during the morning, and this certainly  
444 has an impact on the daily patterns of activity one may infer based on recordings in sound  
445 collections. Our data and recordings in sound collections reveal that tropical birds exhibit  
446 varying strategies in vocal activity through the day (Figure 2, Figure S1); some species  
447 sing in the early morning and late afternoon, others during the whole morning, and a few  
448 probably during the whole day. Therefore, to the valuable recommendations for recording  
449 bird sounds offered by previous workers (Parker III 1991; Budney and Grotke 1997), we  
450 would add the importance of recording constantly along the day and of recording as many  
451 singing birds as possible. By doing so, recordists may considerably increase the  
452 usefulness of their material for studies on various aspects of avian biology.

453

454 The idea that one may use information in sound collections to study vocal seasonality  
455 along the year as shown by our analyses focused on Great Tinamou and Clay-colored  
456 Thrush offers exciting opportunities for future study. For example, information in sound

457 collections may allow one to assess the effect of climate on singing behavior within and  
458 across sites; because singing correlates with reproduction, information in sound  
459 collections may further be used as a proxy to examine geographic variation in breeding  
460 activity and its consequences for population differentiation (Quintero et al. 2014). In the  
461 long term, sound recordings in collections may allow one to monitor changes in vocal  
462 activity patterns and annual phenological cycles in wild bird populations in relation to  
463 local and global change.

464

465 We conclude that recordings in sound collections contain valuable information about the  
466 vocal output of birds, which opens the possibility of considering vocal output as a  
467 variable of interest in studies on the ecology and evolution of birds and other animals that  
468 use acoustic signals for communication. Sound collections also contain much information  
469 about temporal patterns in vocal activity over various time frames; this information is  
470 relevant to studies in many areas of animal biology. Just as traditional museum specimens  
471 capture valuable information about the time in which they were collected (Pyke and  
472 Ehrlich 2010), properly archived sound recordings may be considered acoustic specimens  
473 with great potential to be used in various ways in the future. Traditional specimens have  
474 been used for purposes that original collectors could not have imagined, including the  
475 documentation of the effects of environmental contaminants (Berg et al. 1966; Ratcliffe  
476 1967) or the prediction of shifts in species distributions as a consequence of climatic  
477 change (Peterson et al. 2002). The same could be true of future studies on vocal activity  
478 and vocal output based on properly curated and publicly available sound collections. Now  
479 that sound recordings are relatively easy to collect and archive, we encourage field

480 researchers to record animal sounds along the day and the year, and to make recordings  
481 and associated information available to the public. To finalize, we emphasize that much  
482 of data one may extract from recordings in sound collections is waiting to be used; part of  
483 the information needed for many different studies is already sitting on the shelf.

484

#### 485 **ACKNOWLEDGMENTS**

486 We thank Chingaza National Park for allowing us to record bird songs. Greg Budney and  
487 Matt Medler of the Macaulay Library of Natural Sounds at Cornell University, and the  
488 Colección de Sonidos Ambientales of the Instituto Alexander von Humboldt gave us  
489 unrestricted access to the information archived in their collections. We thank to Ken  
490 Rosenberg of the Cornell Lab of Ornithology for the loan of some recording equipments.  
491 We thank all the recordists who have deposited their recordings in these archives and  
492 who have made them available through xeno-canto. We are grateful to Laura Céspedes,  
493 Simón Quintero, Juan Ignacio Areta, Mecky Holzmann, Trevor Price and Alex Kirschel  
494 for assistance in the field.

495

#### 496 **REFERENCES**

497 Aide TM, Corrada-Bravo C, Campos-Cerqueira M, Milan C, Vega G, Alvarez R. 2013.  
498 Real-time bioacoustics monitoring and automated species identification. PeerJ 1:e103.  
499 Antunes AZ. 2008. Diurnal and seasonal variability in bird counts in a forest fragment in  
500 southeastern Brazil. Rev. Bras. Zool. 25:228–237.

- 501 Arvidsson BL, Neergaard R. 1991. Mate choice in the willow warbler - a field  
502 experiment. *Behav. Ecol. Sociobiol.* 29:225–229.
- 503 Ballentine B. 2004. Vocal performance influences female response to male bird song: an  
504 experimental test. *Behav. Ecol.* 15:163–168.
- 505 Berg KS, Brumfield RT, Apanius V. 2006. Phylogenetic and ecological determinants of  
506 the neotropical dawn chorus. *Proc. R. Soc. B Biol. Sci.* 273:999–1005.
- 507 Berg W, Johnels A, Sjostrand B, Westermarck T. 1966. Mercury content in feathers of  
508 Swedish birds from the past 100 years. *Oikos* 17:71–83.
- 509 Blake JG. 1992. Temporal variation in point counts of birds in a lowland wet forest in  
510 Costa Rica. *Condor* 94:265–275.
- 511 Borchert R. 1996. Phenology and flowering periodicity of Neotropical dry forest species:  
512 evidence from herbarium collections. *J. Trop. Ecol.* 12:65-80.
- 513 Botero CA, Rossman RJ, Caro LM, Stenzler LM, Lovette IJ, De Kort SR, Vehrencamp  
514 SL. 2009. Syllable type consistency is related to age, social status, and reproductive  
515 success in the Tropical Mockingbird. *Anim. Behav.* 77:701–706.
- 516 Boulter SL, Kitching RL, Howlett BG. 2006. Family, visitors and the weather: Patterns of  
517 flowering in tropical rain forests of northern Australia. *J. Ecol.* 94:369–382.
- 518 Budney GF, Grotke RW. 1997. Techniques for audio recording vocalizations of tropical  
519 birds. *Ornithol. Monogr.* 48:147–163.

- 520 Cardoso GC, Hu Y. 2011. Birdsong performance and the evolution of simple (rather than  
521 elaborate) sexual signals. *Am. Nat.* 178:679–686.
- 522 Chiver, I., Stutchbury, B. J. M., & Morton, E. S. 2015. The function of seasonal song in a  
523 tropical resident species, the Red-throated Ant-tanager (*Habia fuscicauda*). *J. Ornithol.*  
524 156: 55-63.
- 525 Derryberry EP, Seddon N, Claramunt S, Tobias JA, Baker A, Aleixo A, Brumfield RT.  
526 2012. Correlated evolution of beak morphology and song in the Neotropical woodcreeper  
527 radiation. *Evolution* 66:2784–2797.
- 528 Eberhardt LS. 1994. Oxygen Consumption During Singing by Male Carolina Wrens  
529 (*Thryothorus ludovicianus*). *Auk* 111:124–130.
- 530 Garamszegi LZ, Moreno J, Møller AP. 2006. Avian song complexity is associated with  
531 high field metabolic rate. *Evol. Ecol. Res.* 8:75–90.
- 532 Gaunt AS, Bucher TL, Gaunt SLL, Baptista LA. 1994. Is singing costly? *Auk* 113:718–  
533 721.
- 534 Gil D, Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits.  
535 *Trends Ecol. Evol.* 17:133–141.
- 536 Gil D, Slater PJB. 2000. Multiple song repertoire characteristics in the willow warbler  
537 (*Phylloscopus trochilus*): correlations with female choice and offspring viability. *Behav.*  
538 *Ecol. Sociobiol.* 47:319–326.



- 539 Hasselquist D, Bensch S. 2008. Daily energy expenditure of singing great reed warblers  
540 *Acrocephalus arundinaceus*. J. Avian Biol. 39:384–388.
- 541 Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of  
542 birds in space and time. Nature 491:444–448.
- 543 Koloff J, Mennill DJ. 2012. Vocal behaviour of Barred Antshrikes, a Neotropical  
544 duetting suboscine bird. J. Ornithol. 154:51–61.
- 545 Kovach Computing Services. 2011. Oriana – Circular Statistics for Windows.
- 546 Krams I. 2001. Communication in crested tits and the risk of predation. Anim. Behav.  
547 61:1065–1068.
- 548 Lancaster DA. 1964. Life History of the Boucard Tinamou in British Honduras Part II:  
549 Breeding Biology. Condor 66:253–276.
- 550 Negret PJ, Garzon O, Stevenson PR, Laverde-R O. 2015. New ecological information for  
551 the Black Tinamou (*Tinamus osgoodi hershkovitzi*). Auk 132:533–539.
- 552 Oberweger K, Goller F. 2001. The metabolic cost of birdsong production. J. Exp. Biol.  
553 204:3379–88.
- 554 Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W. 2012. Caper:  
555 comparative analyses of phylogenetics and evolution in R.
- 556 Parker III TA. 1991. On the use of tape recorders in avifaunal surveys. Auk 108:443–444.

- 557 Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddenmeier  
558 RH, Stockwell DRB. 2002. Future projections for Mexican faunas under global climate  
559 change scenarios. *Nature* 416:626–629.
- 560 Podos J. 1997. A performance constraint on the evolution of trilled vocalizations in a  
561 songbird family (Passeriformes: Emberizidae). *Evolution* 51:537–551.
- 562 Pyke GH, Ehrlich PR. 2010. Biological collections and ecological/environmental  
563 research: A review, some observations and a look to the future. *Biol. Rev.* 85:247–266.
- 564 Quintero I, González-Caro S, Zalamea P-C, Cadena CD. 2014. Asynchrony of seasons:  
565 genetic differentiation associated with geographic variation in climatic seasonality and  
566 reproductive phenology. *Am. Nat.* 184:352–363.
- 567 Ratcliffe DA. 1967. Decrease in eggshell weight in certain birds of prey. *Science*  
568 215:208–210.
- 569 Read AF, Weary DM. 1992. The evolution of bird song : comparative analyses. *Philos.*  
570 *Trans. R. Soc. B Biol. Sci.* 338:165–187.
- 571 Rempel RS, Francis CM, Robinson JN, Campbell M. 2013. Comparison of audio  
572 recording system performance for detecting and monitoring songbirds. *J. F. Ornithol.*  
573 84:86–97.
- 574 Ridgely RS, Allnutt TF, Brooks T, McNicoll DK, Mehlman DW, Young BE, Zook JR.  
575 2003. Digital Distribution Maps of the Birds of the Western Hemisphere, version 1.0.  
576 NatureServe, Arlington, Virginia, USA.

- 577 Shutler D. 2011. Sexual selection: when to expect trade-offs. *Biol. Lett.* 7:101–104.
- 578 Slater PJB. 2003. Fifty years of bird song research: a case study in animal behaviour.  
579 *Anim. Behav.* 65:633–639.
- 580 Stiles FG, Rosselli L. 1998. Inventario de las aves de un bosque altoandino: comparación  
581 de dos métodos. *Caldasia* 20:29–43.
- 582 Stutchbury BJM, Morton ES. 2001. Behavioral ecology of tropical birds. Academic  
583 Press.
- 584 Topp SM, Mennill DJ. 2008. Seasonal variation in the duetting behaviour of rufous-and-  
585 white wrens (*Thryothorus rufalbus*). *Behav. Ecol. Sociobiol.* 62:1107–1117.
- 586 Vargas O, Pedraza P. 2004. Parque Nacional Natural Chingaza. Bogotá, D. C.: Gente  
587 Nueva Editorial.
- 588 Ward S. 2004. Singing is not energetically demanding for pied flycatchers, *Ficedula*  
589 *hypoleuca*. *Behav. Ecol.* 15:477–484.
- 590 Wikelski M, Hau M, Wingfield J. 2000. Seasonality of reproduction in a Neotropical rain  
591 forest bird. *Ecology* 81:2458–2472.
- 592 Woodgate JL, Mariette MM, Bennett ATD, Griffith SC, Buchanan KL. 2012. Male song  
593 structure predicts reproductive success in a wild zebra finch population. *Anim. Behav.*  
594 83:773–781.

595 Zalamea P-C, Munoz F, Stevenson PR, Paine CET, Sarmiento C, Sabatier D, Heuret P.

596 2011. Continental-scale patterns of *Cecropia* reproductive phenology: evidence from

597 herbarium specimens. Proc. Biol. Sci. 278:2437–2445.

598

599

600

601

602

603

604

605

606

607

608

609

610 Table 1. Number of recordings of avian vocalizations obtained through continuous  
611 monitoring by month and elevation in Chingaza National Park from February to August  
612 2013.

<b>ARU No</b>	<b>February</b>	<b>April</b>	<b>May</b>	<b>July</b>	<b>August</b>	<b>Total</b>	<b>Geographical Coordinates</b>	<b>Elevation (m)</b>
<b>1</b>	248					248	4°41'47"; 73°50'53"	2950
<b>2</b>	121	138	92			351	4°41'54"; 73°50'50"	2960
<b>3</b>	158					158	4°42'08"; 73°50'50"	3015
<b>4</b>	233		121	246	246	846	4°41'44"; 73°50'39"	3030
<b>5</b>		88	38			127	4°41'27"; 73°50'24"	3015
<b>6</b>		131	132	150	50	465	4°42'42"; 73°50'21"	3170
<b>Total</b>	760	427	383	396	296	2192		

613

614

615

616

617

618

619

620

621

622

623 Table 2. Number of recordings obtained via continuous monitoring using ARUs in  
 624 Barbacoas and Bahía Málaga and number of recordings found in the xeno-canto (XC)  
 625 archive of lowland species used to study daily patterns of vocal activity.

<b>Family</b>	<b>Species</b>	<b>ARU</b>	<b>XC</b>	<b>Total</b>
Tinamidae	<i>Tinamus major</i>	31	55	86
Cracidae	<i>Ortalis columbiana</i>	60	29	89
Columbidae	<i>Patagioenas cayennensis</i>	116	41	157
Columbidae	<i>Patagioenas speciosa</i>	102	83	185
Ramphastidae	<i>Ramphastos ambiguus</i>	95	107	202
Thamnophilidae	<i>Thamnophilus atrinucha</i>	69	94	163
Thamnophilidae	<i>Myrmeciza exsul</i>	74	238	312
Thamnophilidae	<i>Myrmeciza berlepschi</i>	48	21	69
Tyrannidae	<i>Mionectes oleagineus</i>	48	68	116
Tyrannidae	<i>Todirostrum nigriceps</i>	63	16	79
Tyrannidae	<i>Tolmomyias flaviventris</i>	165	177	342
Tyrannidae	<i>Attila spadiceus</i>	33	325	358
Pipridae	<i>Lepidothrix coronata</i>	83	63	146
Pipridae	<i>Manacus manacus</i>	95	118	213
Trogloditidae	<i>Pheugopedius fasciatoventris</i>	62	39	101
	<b>Total</b>	1144	1474	2618

626

627

628

629

630

631

632

633 Table 3. Results of Watson-Williams circular tests for differences between the  
634 distributions of recordings obtained via continuous monitoring and based on recordings  
635 deposited in the xeno-canto archive (see Figure 2). Except for three species (two pigeons  
636 and one toucan shown in bold), daily activity patterns obtained via continuous monitoring  
637 and based on information in xeno-canto did not differ, validating the use of information  
638 in sound archives.

Family	Species	Watson-Williams F-test
Tinamidae	<i>Tinamus major</i>	1.999
Cracidae	<i>Ortalis colombiana</i>	2.978
Columbidae	<i>Patagioenas cayennensis</i>	<b>5.662 *</b>
Columbidae	<i>Patagioenas speciosa</i>	<b>16.768 ***</b>
Ramphastidae	<i>Ramphastos ambiguus</i>	<b>16.95 ***</b>
Thamnophilidae	<i>Thamnophilus atrinucha</i>	4.233
Thamnophilidae	<i>Myrmeciza exsul</i>	0.752
Thamnophilidae	<i>Myrmeciza berlepshchi</i>	1.029
Tyrannidae	<i>Mionectes oleagineus</i>	0.649
Tyrannidae	<i>Todirostrum nigriceps</i>	0.288
Tyrannidae	<i>Tolmomyias flaviventris</i>	0.064
Tyrannidae	<i>Attila spadiceus</i>	3.639
Pipridae	<i>Lepidothrix coronata</i>	0.72
Pipridae	<i>Manacus manacus</i>	0.48
Troglodytidae	<i>Pheugopedius fasciatoventris</i>	1.523

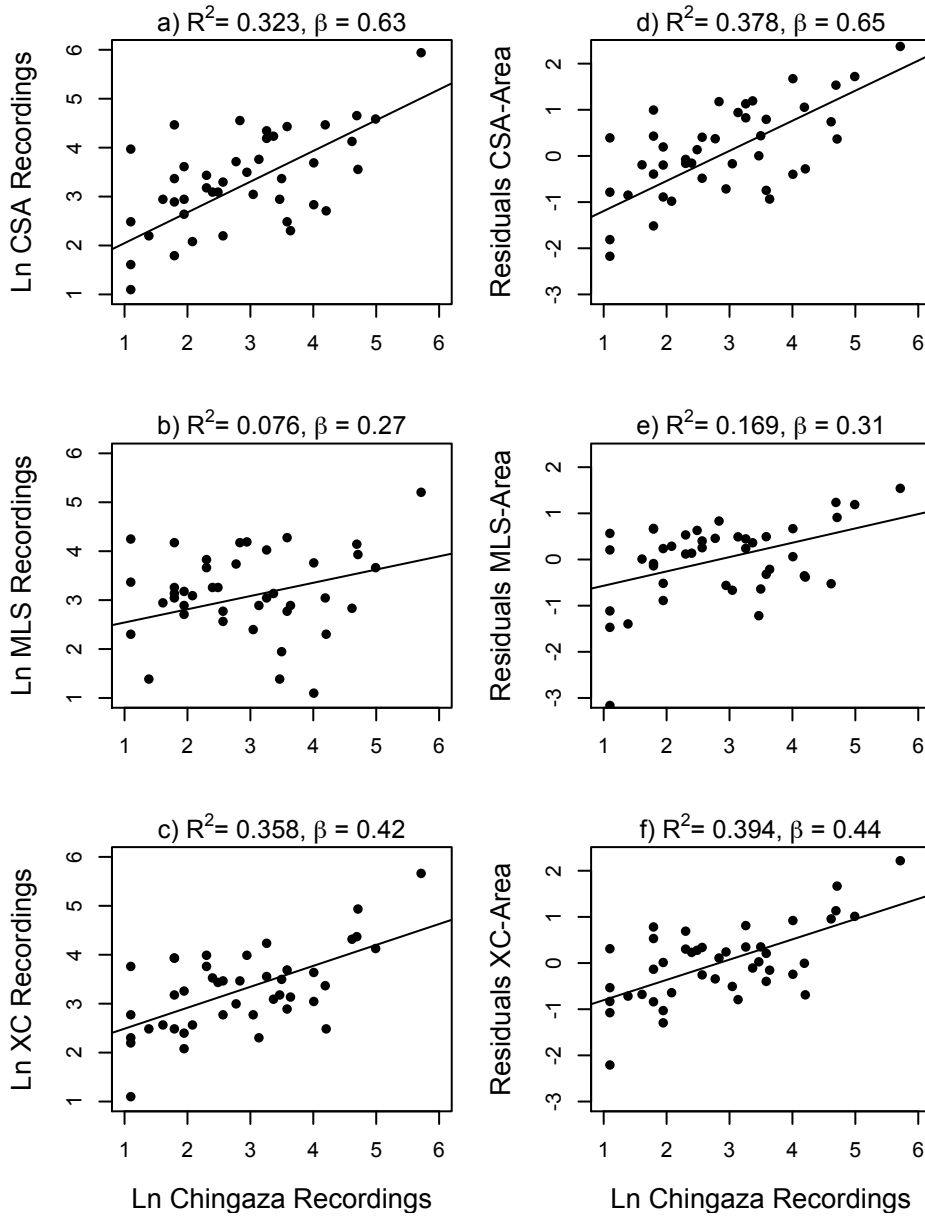
639

640

641

642 Figure 1. Relationships between vocal output estimated through continuous monitoring  
643 based on recordings obtained in Chingaza and the number of recordings archived in  
644 sound collections (1a – 1c), and the residual number of recordings in sound collections  
645 unaccounted for by area of distributional range (1d – 1f). Results of linear regression  
646 analyses are significant in all cases, but note the increased fit of models when accounting  
647 for area of distributional range. These patterns suggest that information in sound archives  
648 is an appropriate proxy of vocal output.





649

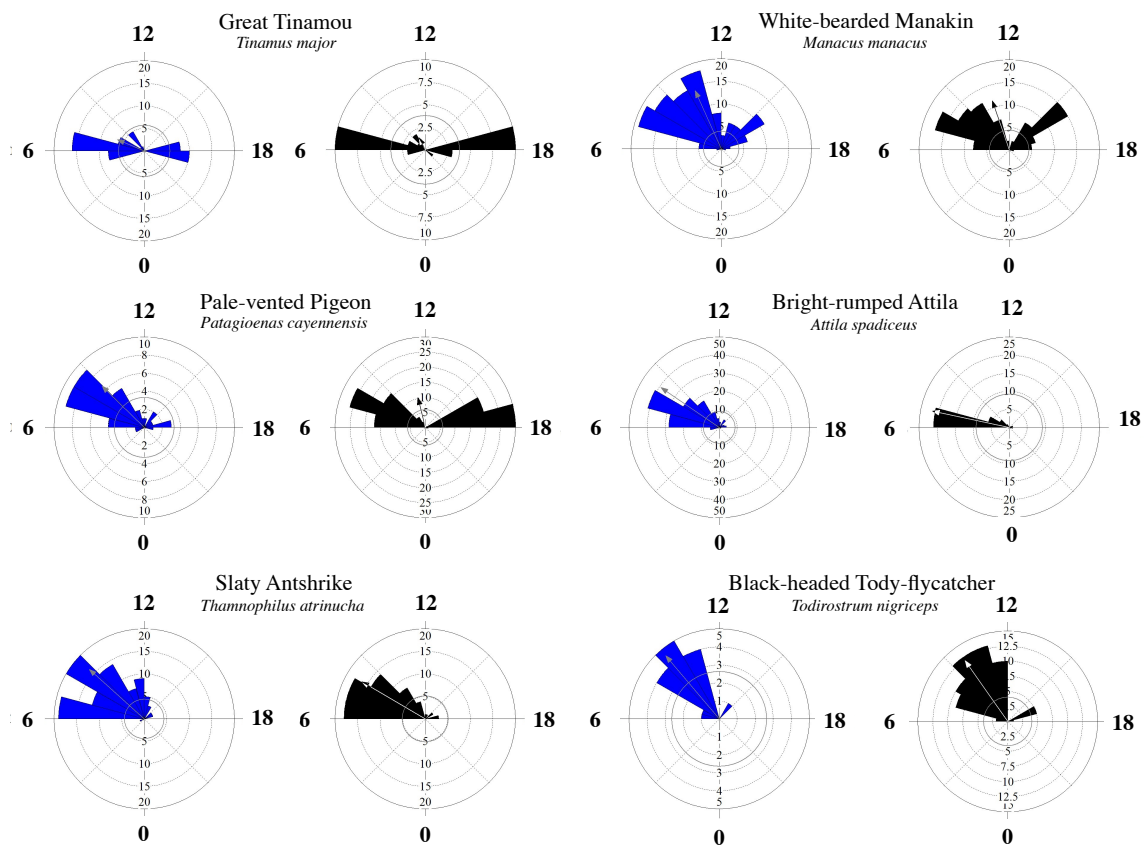
650

651

652

653

654 Figure 2. Circular plots showing daily vocal activity for six lowland species estimated via  
655 continuous monitoring (black) and based on recordings deposited in the xeno-canto  
656 archive (blue). We selected six of the 15 species studied to illustrate general patterns  
657 observed in the data. Note the strong similarity between sources of data in patterns in all  
658 species except for the Pale-vented Pigeon (*Patagioenas cayennensis*), in which the  
659 information in xeno-canto failed to detect a peak in singing activity revealed through  
660 continuous monitoring.

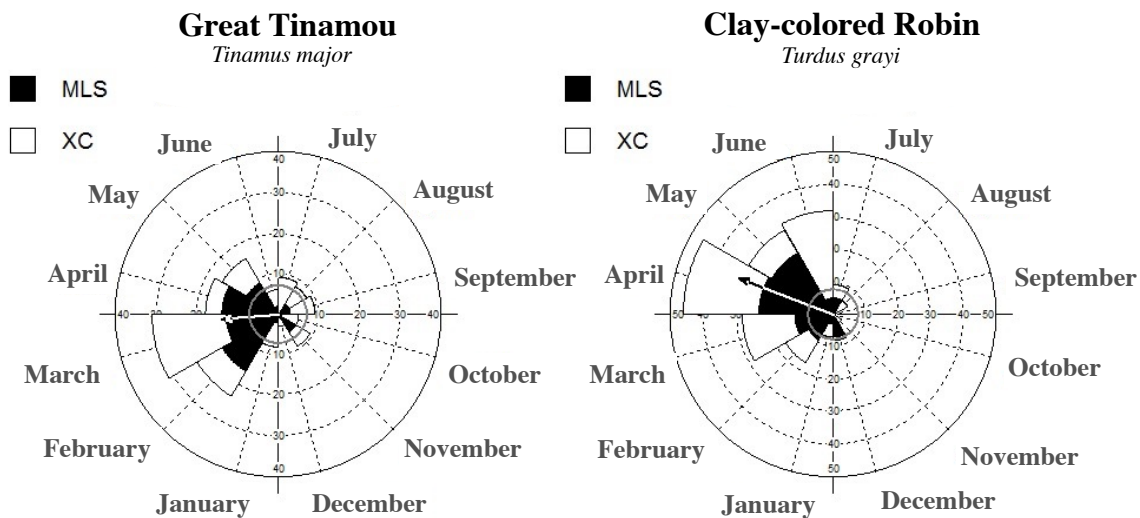


661

662

663

664 Figure 3. Circular plots showing annual vocal activity for the Great Tinamou and the  
665 Clay-colored Thrush in the Northern Hemisphere. Data from the MLS are shown in black  
666 and data from XC in white. Note that estimated vocal activity is very similar based on the  
667 information obtained from the two collections for both species: Great Tinamou vocal  
668 activity peaks between March and April and Clay-colored Robin vocal activity peaks in  
669 April; these patterns coincide with patterns reported in the literature based on systematic  
670 monitoring (see text).



671