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1 **The song of the Cinnamon-breasted Bunting, *Emberiza tahapisi*, in**  
2 **the Bamenda Highlands (NW Cameroon)**

3

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5

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9

10 *Running title:* Song of the cinnamon-breasted bunting

11

12

13 **Abstract**

14 In this study, I describe the song of the Cinnamon-breasted Bunting (*Emberiza*  
15 *tahapisi*) - a common and widespread species in sub-Saharan. Several aspects of song  
16 behaviour were addressed based on recordings of 58 males in the Bamenda Highlands  
17 (NW Cameroon). The song of the cinnamon-breasted bunting is discontinuous and  
18 consists of short (1.2 s on average), relatively broadband (range 2.5 – 9.2 kHz)  
19 strophes repeated at a highly variable rate (2 - 14 strophes per minute). Each male  
20 sang a single song type consisting of 4 to 9 different syllable types. Syllable types  
21 differed in acoustic structure, and I describe a total of 40 discrete types. At the song  
22 type level, only 8 different song types were found. Males from local groups tended to  
23 have slightly more similar songs than strangers separated by a distance of more than  
24 500 m. However, males with shared song types clearly did not aggregate. All males  
25 within the studied population shared a characteristic final whistle syllable, which  
26 resemble some other buntings. The birds sang from locations elevated above the  
27 surrounding vegetation, usually from trees or rocks. I found no significant relationship  
28 between song rate, time after sunrise, time of season and song post height.

29 *Key words:* song complexity, microgeographic variation, song rate, song post,  
30 repertoire size, dialect cue

31

32 **Zusammenfassung**

33 **Der Gesang der Bergammer (*Emberiza tahapisi*) im Bamenda-Hochland von**  
34 **Nordwest-Kamerun**

35

36 In dieser Arbeit beschreibe ich den Gesang der Bergammer, einer in den Ländern  
37 südlich der Sahara häufigen und weit verbreiteten Art. Anhand der Aufnahmen von  
38 58 Männchen aus dem Bamenda-Hochland (NW-Kamerun) werden die Aspekte ihres  
39 Sing-Verhaltens untersucht. Der Gesang dieser Art ist nicht zusammenhängend,  
40 sondern besteht aus kurzen, im Schnitt 1,2 Sekunden dauernden, relativ breitbandigen  
41 (2,5 – 9,2 kHz) Strophen, die mit einer hohen Variabilitätsrate wiederholt werden (2 –  
42 14 Strophen pro Minute). Jedes einzelne Männchen sang einen einzigen Gesangs-Typ  
43 aus 4 – 9 unterschiedlichen Silben-Typen, die sich in ihrem akustischen Aufbau

44 unterschieden; ich beschreibe 40 eigene derartige Typen. Bei den Gesangs-Typen  
45 konnten nur 8 Typen gefunden werden. Männchen innerhalb lokaler Gruppen zeigten  
46 etwas ähnlichere Gesänge als fremde Männchen in Entfernungen von mehr als 500  
47 Metern; aber Männchen mit gemeinsamen Gesangs-Typen kamen nicht unbedingt  
48 zusammen vor. Alle Männchen der untersuchten Population hatten eine Pfeif-Silbe  
49 am Schluss gemeinsam, die an einige andere Ammern-Arten erinnerte. Die Vögel  
50 sangen an Stellen, die höher als die umgebende Vegetation lagen, in der Regel Felsen  
51 oder Bäume. Ich fand keinen signifikanten Zusammenhang zwischen der Gesangs-  
52 Rate, der seit Sonnenaufgang verstrichenen Zeit, der Jahreszeit und der Höhe des  
53 Gesangsplatzes.

54

## 55 **Introduction**

56 Song is a sexually selected trait that plays a crucial role in mate attraction and  
57 resource defence in birds (Catchpole & Slater 2008). Therefore, it has attracted the  
58 attention of biologists for decades and is probably one of the most thoroughly studied  
59 models of socially transmitted behaviour. Impressive progress has been made in the  
60 science of bird songs in the last 50 years in terms of mechanisms of song production,  
61 learning and its neurobiological background and detailed analyses of song variation  
62 patterns in time and space (Slater 2003). This growth of knowledge has a double  
63 effect: we know more about song behaviour, but we also can determine the most  
64 important gaps in our knowledge that hinder our understanding of song evolution and  
65 ecology. One issue is the amount and uneven distribution of data on song behaviour.  
66 We know a lot about the song of very few species that have become intensively  
67 studied models, whereas we only have rudimentary data for hundreds of species. A  
68 special case is birds from the tropics. The majority of modern bird species live in  
69 tropical or subtropical areas. The tropics were also localised centres of bird evolution.  
70 Therefore, the early evolution of song also occurred in the tropics. However, the  
71 majority of the studies on bird song have been conducted in temperate areas, although  
72 some tropical song phenomena as (e.g., duetting) have been recognised relatively  
73 recently (Hall 2009). Bird songs from tropical Africa are the least studied, and there is  
74 still a paucity of data for most of the species, including common and widespread  
75 species. This problem concerns also birds, which started large radiation in open  
76 habitats in the temperate zone and then colonized into tropics. Here the genus  
77 *Emberiza* is a good example (Klicka et al. 2003, Alström et al. 2008), as our  
78 knowledge is heavily biased towards temperate zone species. An interspecific  
79 comparison in such a taxon gives good opportunities to track changes in song  
80 behaviour, which likely appeared after colonization of the areas with different  
81 climatic conditions and habitats.

82         Emberizidae (sparrows, buntings and their relatives) are among the most  
83 diverse families in terms of number of species among birds. Emberizids are found on  
84 all continents except Australia and Antarctica and have the highest diversity in the  
85 Western Hemisphere (Byers et al. 1995). The genus *Emberiza* consists of about 40  
86 living species inhabiting the different, typically open habitats of Eurasia. Only a few  
87 species have limited distribution in Africa. The acoustic communication of some

88 *Emberiza* species has been intensively studied. Most of these descriptive studies have  
89 focussed on different aspects of song variation in space (Møller 1982, Hansen 1985,  
90 McGregor 1986, Glaubrecht 1989, 1991, Matessi et al. 2000, Osiejuk & Ratyńska  
91 2003, Caro et al. 2009, Wonke & Wallschläger 2009). Other experimental studies  
92 have addressed questions related to dialect function and mechanisms of dialect  
93 recognition (Pellerin 1983, Hansen 1984, Baker et al. 1987, Osiejuk et al. 2007a). The  
94 other aspects of song behaviour that have been investigated are territorial defence  
95 (Kreutzer & Güttinger 1991, Nemeth 1996, Osiejuk et al. 2007b, Suter et al. 2009),  
96 neighbour-stranger recognition (Hansen 1984, Skierczyński et al. 2007, Skierczyński  
97 & Osiejuk 2010) and male-female communication (Nemeth 1994, Wingelmaier et al.  
98 2007). However, in these studies ornithologists have focussed on only five common  
99 European species: corn buntings, *E. calandra*; ortolan buntings, *E. hortulana*;  
100 yellowhammer buntings, *E. citrinella*; ciril buntings, *E. cirilus*; and reed buntings, *E.*  
101 *schoeniclus*. For the rest of the *Emberiza* species we have only rudimentary data that  
102 hinders the possibility of comparative studies on song evolution in *Emberiza* and their  
103 relatives. The particularly understudied species are those limited to eastern Asia and  
104 all African species (Byers et al. 1995).

105         Here I describe song structure, syllable repertoire variation and singing  
106 behaviour of the cinnamon-breasted bunting (*Emberiza tahapisi goslingi*). To my  
107 knowledge this is the first study on the song behaviour of this species, despite it being  
108 one of the most common and widespread of the African buntings (Byers et al. 1995).  
109 This study is the first step to a better understanding of changes in song behaviour,  
110 which likely occurred during and after colonization of Afrotropics in Emberizids.

111

112 **Material and methods**

113

114 *Study area*

115 The study was conducted in November and December of 2008 (the beginning of the  
116 dry season) approximately 6 km southeast of Big Babanki village in the Bamenda  
117 Highlands, Northwest Region, Cameroon. The study area was spread between 6° 5'  
118 8" - 6° 6' 40" N and 10° 17' 45" - 10° 19' 77" E (altitude range 1928-2358 m a.s.l.,  
119 average altitude 2178 m a.s.l., area surveyed ca. 6 km<sup>2</sup>). The Bamenda Highlands are  
120 one of the most important hotspots of bird diversity and endemism in Africa (Orme et  
121 al. 2005). However, intensive logging has reduced formerly continuous forests to  
122 isolated patches in recent decades (ICBP 2002). At present, the vegetation covering  
123 the study area consists of mosaics of montane forest patches, shrubby corridors,  
124 grasslands and vegetable plantations (at a lower altitude than the study site).

125 The cinnamon-breasted bunting prefers intensively grazed pastures dominated  
126 by grasslands and rocky grasslands and, to some extent, also inhabits gentle rocky  
127 slopes with bare soil available (Byers et al. 1995, Sedláček et al. 2007, personal obs.).  
128 There is no systematically collected data available on the occurrence of the cinnamon-  
129 breasted bunting in this region, but it is likely that forest fragmentation in the  
130 Bamenda Highlands has increased the habitat area preferred by this species. In a  
131 recent survey of birds in the same study area, Sedláček et al. (2007) found that the  
132 cinnamon-breasted bunting is a common species (with a category of abundance of 3-4  
133 according to the classification of Stuart & Jensen 1986) that is resident to the area.  
134 The peak of its breeding is most likely at the beginning of the dry season.

135

136 *Recording of birds*

137 Birds were recorded between 16 November and 14 December 2008, preferably during  
138 the morning (0600-1200 hrs) and evening (1600-1800 hrs). However, singing birds  
139 were observed at almost every time of the day. Furthermore, on cloudy days with  
140 lower temperature some birds were also recorded at 1200 hrs and 1600 hrs. During  
141 the study, the area was surveyed each day for 8-10 hours. Although I was not focused  
142 only on the detection of cinnamon-breasted buntings, I tried to survey each habitat

143 patch that seemed to be suitable for that species. Patches were chosen based on aerial  
144 photos and visual inspection of the area from surrounding hills.

145           Birds were recorded using a Marantz PMD660 solid-state recorder with a  
146 Sennheiser ME 67 shotgun microphone (K6 powering unit and MZW67PRO  
147 windscreen). All recordings were mono-linear PCM WAV of 48-kHz sampling  
148 frequency and 16-bit resolution. Geographic coordinates and a.s.l height of all males  
149 were measured using a Garmin GPSMap 76 CSx receiver. In sites with a higher  
150 density of males, recordings were preceded by the intensive observation of all males  
151 and preparing sketch maps of their song posts, including information about location of  
152 simultaneously singing males. Then, all birds were recorded on one day, and special  
153 attention was paid to the location of song posts of all neighbours during recording.  
154 This ensured the identification of different males. Beside the location of the subject  
155 male, each recording was given a unique number and the following data were  
156 recorded: time, behaviour of the subject (song, calls etc.), context (counter-singing,  
157 solo singing) and song post characteristics (sitting place, height of sitting place and  
158 height of surrounding vegetation). In some cases it was not possible to collect all data.  
159 Therefore, sample size differed for analyses of particular variables.

160

#### 161 *Sound analysis and bioacoustics terms*

162 Sonograms of songs were analysed using Avisoft SASLab Pro 4.52 software (Specht  
163 2002) with the following set of parameters: 512 FFT-length, frame (%) = 75, window  
164 = hamming and temporal overlap= 75%. This provided a sonogram of 162 Hz  
165 bandwidth with 94-Hz frequency and 2.67-ms time resolution.

166           Preliminary analysis revealed that cinnamon-breasted buntings sing short,  
167 simple song phrases, repeated in a very stereotyped manner for each male. Because  
168 the acoustic character of sounds forming the songs was similar to the intensively  
169 studied white-crowned sparrow, *Zonotrichia leucophrys*, I applied a similar  
170 terminology to describe the song structure and its variation (e.g., Nelson 2000). I  
171 defined a note as a continuous tracing on a sonogram separated from other notes by at  
172 least 3 ms of silence. Single notes or group of notes always occurring together built  
173 minimal units of sound production called “syllables”. Syllables were comparable both



174 between performances of each male and between different males, regardless of their  
175 occurrence as single syllables or a repeated sequence (e.g., a trill) (Fig. 1).

176 Each recognised syllable type was analysed in detail and categorised to a  
177 particular type of sound from an acoustic perspective (see Fig. 1). A “whistle” was  
178 defined as a single note with one dominant frequency and no amplitude modulation  
179 (i.e., pure whistle). A “buzz” was considered to be a complicated note or group of  
180 notes that always clearly contained an amplitude modulated whistle. A “complex  
181 syllable” was defined as a group of short whistle notes of different frequency in a time  
182 domain that always occurred together as a group separated from other syllables. Some  
183 types of whistles and complex syllables occurred exclusively in groups forming  
184 characteristic trills, while others always occurred as single syllables. Therefore, I used  
185 the following terms and abbreviations: whistle (W), buzz (B), complex syllable (C)  
186 and trill (T) (Fig. 1). For example, a typical song could be built with a sequence of T-  
187 T-B-B-B-C-W, meaning that the song started with two different trills followed by  
188 three different buzzes and was finished with a complex syllable and a single whistle.  
189 This acoustic description allowed me to present results on song structure to describe  
190 the song syntax of cinnamon-breasted buntings.

191 Songs of cinnamon-breasted buntings consisted of several different syllable  
192 types belonging to the acoustic categories mentioned above. To describe songs in a  
193 way that allowed for the comparison of syllable repertoires, I used syllables as  
194 minimal units of song production and divided each song into a sequence of different  
195 syllable types (as in Osiejuk et al. 2003 for the Ortolan Bunting). Each syllable on a  
196 sonogram recognised as a new type received its own symbolic representation as a  
197 letter or a letter with number subscript. For example, a song described as a-b-c-d-e-f-g  
198 consisted of seven different syllable types that occurred exactly in that order within  
199 the song phrase (Fig. 1). Syllables were clearly separated by gaps and occurred as  
200 single examples or in series of the same kind (trills).

201 The initial inspection of sonograms revealed that each male was most always  
202 singing songs consisting of exactly the same sequence of syllables. The only within-  
203 individual variation in song structure concerned omitting some syllables and thereby  
204 shortening the song. In the majority of cases, males omitted some initial syllables or  
205 trills or ceased singing in the middle of the song phrase. Shortening of the song was  
206 common but not very frequent with respect to the number of all songs recorded. It was

207 also clear that some males shared the majority of syllable sequences regardless of  
208 shortening songs from time to time and that the shortened versions should not be  
209 counted as separate song types. The shortening was either caused by the observer  
210 effect or might reflect aggressive interactions with a rival. Therefore, I primarily tried  
211 to identify different song types (defined as a group of songs that consisted of the same  
212 syllables arranged in the same order) based on the most complete versions of the song  
213 performed by particular males. For example, several males sang full songs with a  
214 sequence of syllables of a-b-c-d-e-f-g but occasionally also produced songs that  
215 consisted of the following sequences: b-c-d-e-f-g, a-b-c-d-e-f or b-c-d-e-f. Such songs  
216 were treated as belonging to the same type with the unchangeable “core” sequence  
217 indicated by brackets around the core syllables, e.g., [b-c-d-e-f].

218

#### 219 *Microgeographic song variation*

220 I analysed microgeographic song variation at two levels. In the first approach, I used  
221 distinguished song types as discrete units based on shared core syllable sequences.  
222 Because each male sang only a single song type, the song type similarity between  
223 males had binary character. In other words, any two males shared (similarity = 1) or  
224 did not share (similarity = 0) their syllable repertoires. In the second approach, I used  
225 the Jaccard index to compare the similarity of songs performed by pairs of males in  
226 detail. The data on the song structure of individual males were used to construct the  
227 similarity matrix using the Jaccard similarity coefficient (J), which covered song  
228 similarity between males with respect to the syllable types of their songs. The Jaccard  
229 coefficient was calculated as  $J = M_{11} / (M_{01} + M_{10} + M_{11})$ , where  $M_{11}$  represents the total  
230 number of shared syllables of the respective song types between a given pair of males  
231 and  $M_{01}$  and  $M_{10}$  represent syllables unique to each of the two males. The coefficient  
232 values ranged from 0 to 1, with  $J = 0$  indicating that the songs of compared males did  
233 not contain any shared syllables and  $J = 1$  indicating that all syllables were shared  
234 between the two males.

235 In both analyses I used 58 males with known song structure and known  
236 geographical position to generate randomly 1000 pairs of males without repetitions.  
237 Binary song type sharing (1 = sharing, 0 = no sharing) and the Jaccard index of song  
238 similarity (0-1) were calculated for each pair. Additionally, I calculated the

239 corresponding matrices of geographic distances between the song posts of males  
240 (between 10 and 4070 m).

241 To illustrate the degree of song sharing in relation to the distance between  
242 males, I compared measures of binary song type sharing and the Jaccard index of  
243 similarity for three types of pairs: pairs within hearing range ( $\leq 250$  m), i.e., familiar  
244 neighbours; pairs within a particular habitat patch (excluding pairs from the first  
245 group), i.e., local groups; and pairs consisting of males from distant patches, i.e.,  
246 strangers (separated by  $> 500$  m). The hearing range distance of 250 m was based on  
247 measurements of distances from which it was possible to hear singing males. The  
248 distance of 500 m for distinguishing between local groups and strangers was based on  
249 the direct measurement of distances between territories. The statistical methods used  
250 in the song sharing analyses are provided below.

251

#### 252 *Statistical analyses*

253 Before each statistical analysis, the distribution of tested variables was assessed, and  
254 then appropriate parametric or nonparametric tests were applied. Correlations between  
255 binary song sharing patterns and the Jaccard index of similarity with distance between  
256 pairs of males were analysed with 1000 bootstrap samples and a Mersene Twister  
257 random number generator. The specific hypotheses on binary song type sharing and  
258 song similarity between neighbours, males from local groups and strangers were  
259 tested using the Monte Carlo permutation procedure (Manly 1997). All tests were  
260 performed using PASW Statistics 18.

261

#### 262 *Material*

263 The study was based on 101 recordings of 58 different males. I recorded  
264 approximately 1100 songs in total, but not all of them were of high enough quality for  
265 subsequent analyses. Once I realised that males sang only one song type, I strived to  
266 record all males within a particular locality rather than collecting recordings that were  
267 as long as possible. Irrespective of this recording strategy, I still collected enough  
268 recordings that were long enough to characterise temporal song variation.

269

270

271 **Results**

272

273 *Song structure and repertoire*

274 Songs of the cinnamon-breasted bunting were short and rarely exceeded 2 seconds  
275 (Table 1). Songs typically covered wide frequency bands between 2.5 and 9.2 kHz  
276 (Table 1). The analysis of all recorded songs revealed that they consisted of 40  
277 different syllable types in total. These different syllable types were classified as  
278 whistles (4), buzzes (15), and complex syllables (21). Ten of these 40 syllable types  
279 always occurred as trills. In nine cases, these trills were built of repeated complex  
280 syllables, and in one case the trill was a repeated whistle. Songs were built of 4 to 9  
281 different syllable types (mean  $\pm$  SE =  $6.5 \pm 0.17$ ). The majority of the songs  
282 contained all described acoustical structures (i.e., whistle, buzz, complex syllable and  
283 trill). Complete songs always began with 1-3 trills that were followed by a sequence  
284 of different buzzes, complex syllables and in some cases a single trill before the  
285 terminal whistle. Each song, except for some shortened performances, was finished  
286 with the same characteristic terminal whistle of declining frequency. This terminal  
287 whistle was described as the “g-whistle” syllable (Fig. 2). Within a song phrase, each  
288 syllable type occurred only in one place in the sequence of syllable types, but some  
289 syllables were repeated and formed trills.

290 Each male sang basically a single song type, and succeeding songs were  
291 identical in most cases. The only observed within-male variations in song structure  
292 concerned deletion of one or more initial syllables, deletion of the final whistle (very  
293 rarely) or insertion/deletion of single syllables in the middle of the song. In the last  
294 case, the deleted or inserted syllables were always very short. Such variations did not  
295 change the hearing impression of the songs. Based on the most complete songs of  
296 each male, I classified all songs into eight different song types, each of which shared  
297 the same core sequence of syllables (Fig. 2). Seven song types were shared by 13, 11,  
298 10, 8, 6, 4 and 4 males, and one song type was unique to a single male.

299

300 *Microgeographic song variation*

301 To analyse the spatial pattern of song type sharing between males, I compared  
302 syllable repertoires and distances for pairs of males with the randomisation procedure  
303 described in the Methods section. Binary song type sharing decreased with distance  
304 (Fig. 3), but the relationship was weak and insignificant (1000 bootstrap  $r_s = -0.03$ ,  $P$   
305  $= 0.325$ ). The probability of shared song types for males within hearing distance ( $\leq$   
306 250 m) was relatively low (approximately 0.2) (Fig. 3). The comparison of song  
307 structure similarity between males with the Jaccard index of similarity revealed  
308 analogous but significant results (1000 bootstrap  $r = -0.11$ ,  $P = 0.001$ , Fig. 4).

309 To test more specific hypotheses, I conducted two self-designed randomisation  
310 tests with the Monte Carlo permutation procedure. First, I tested differences in binary  
311 song type sharing among pairs of males being neighbours, belonging to the same local  
312 group and being strangers (i.e., belonging to different groups). I found significant  
313 differences in binary song type sharing between these three categories (Fig. 3,  
314 Kruskal-Wallis  $\chi^2_2 = 6.19$ ,  $P = 0.046$ ). Similarly, I found significant differences  
315 between the same three categories with the Jaccard similarity Index (ANOVA,  $F_{2,997} =$   
316  $13.925$ ,  $P < 0.001$ ). The Bonferroni post hoc test revealed significant differences  
317 between song similarity of neighbours and strangers ( $P < 0.001$ ) and males belonging  
318 to a local group and strangers ( $P = 0.004$ ), while there was no significant difference  
319 between neighbours and males within a local group ( $P = 1$ ). Regardless of the  
320 statistical significance of differences, average differences between all groups were  
321 small, and birds within local groups did not share syllable repertoires as a whole (Fig.  
322 3-4). However, all recorded males shared the final g-whistle.

323

#### 324 *Song posts and rate of singing*

325 I collected partial data for song post characteristics of 68 recordings (no more than 2  
326 per male). Most birds sang from exposed places on trees, shrubs or rocks (Table 2).  
327 Trees and shrubs used as song posts were often dead (34%,  $n = 38$ ). Song post height  
328 varied between 0 and 19 m (average  $\pm$  SE =  $4.3 \pm 0.59$  m and  $n = 53$ ). Song posts  
329 were located significantly higher (Wilcoxon signed-rank test:  $Z = -4.501$ ,  $n = 48$ ,  $p <$   
330  $0.001$ ) than the surrounding vegetation (0-8 m,  $1.7 \pm 0.33$  m,  $n = 48$ ). Males singing  
331 from high trees did not tend to sing from the highest possible place. Rather, they sang  
332 from places slightly above the level of surrounding vegetation (1-3 m).

333 Cinnamon-breasted bunting males were quite agile and often changed singing  
334 locations or sang when walking and foraging on the ground. Such behaviour was not a  
335 result of the observer effect because birds that were observed from a distance through  
336 binoculars were equally mobile. Moreover, the song rate calculated for all recordings  
337 of acceptable quality ( $n = 86$ ) had a highly skewed distribution (K-S test,  $Z = 2.45$ ,  $p$   
338  $< 0.001$ ) and correlated significantly with the recording duration ( $r = -0.30$ ,  $n = 86$ ,  $p$   
339  $= 0.005$ ). Therefore, I only extracted song rates from recordings exceeding one minute  
340 in duration, during which birds were clearly concentrated on singing. Song rates  
341 measured for these recordings were normally distributed (K-S test,  $Z = 0.485$ ,  $p =$   
342  $0.973$ ) and did not correlate significantly with the duration of the recordings ( $r = -$   
343  $0.18$ ,  $n = 47$ ,  $p = 0.213$ ). The measured song rate varied between 2.8 and 14.2 songs  
344 per minute (average  $\pm$  SE =  $7.4 \pm 0.34$  songs per minute).

345 I found no significant relationships between song rate, day of the season, time  
346 after sunrise, or song post height (all  $p$  for Spearman's rho between 0.222 and 0.740).  
347 Likewise, I did not find any significant relationships in a linear regression model  
348 including all three variables ( $F_{3,17} = 0.025$ ,  $p = 0.994$ ).

349

350

351 **Discussion**

352

353 *Song structure and repertoire size*

354 The songs of birds in the genus *Emberiza* are not among the most elaborate songs  
355 known. The majority of species are discontinuous singers with short song phrases and  
356 small repertoires. Thus, the cinnamon-breasted rock bunting seems to be a typical  
357 *Emberiza* singer. The song phrase complexity in *Emberiza* species is quite variable.  
358 There are species such as the curl bunting, whose songs consist of a trill as a repetition  
359 of a single syllable type, thus representing the lowest level of phrase versatility  
360 (Kreutzer & Güttinger 1991). In contrast, the corn bunting has highly complex song  
361 phrases that sometimes consist of dozens of different elements produced very rapidly  
362 in time (McGregor 1986, Osiejuk & Ratyńska 2003). The cinnamon-breasted rock  
363 bunting has 4-9 different syllable types occurring only once (as a trill or single  
364 syllable) within a song phrase and thus forms songs of quite high complexity (the  
365 ratio between number of different syllables and the total number of syllables within a  
366 song strophe).

367 My results clearly indicate that the song type repertoire of the cinnamon-  
368 breasted bunting is extremely small, as all males sang only one single song type.  
369 However, I observed some differences between successive performances of songs in  
370 particular males. The differences were always small modifications (e.g., omitting a  
371 single syllable or shortening the song) and should not be regarded as separate song  
372 types. Similar small variations have been observed in other species with single song  
373 type repertoires (e.g., treecreepers *Certhia* sp., Thielcke 1992, Osiejuk & Kuczyński  
374 2003).

375

376 *Microgeographic song variation*

377 Two characteristic findings were related to microgeographic song variation in  
378 cinnamon-breasted buntings. First, all males within the studied population shared the  
379 same final syllable of song. This final syllable was a very characteristic whistle (g-  
380 whistle) that has the longest duration among all 40 syllables described (Fig. 1-2).  
381 Such a pattern is very similar to those found for several other bunting species, because



382 buntings often share a specific song structure over larger areas. For example,  
383 yellowhammer bunting males share specific final whistles within dialect areas (Møller  
384 1982, Hansen 1985, Glaubrecht 1989, 1991, Rutkowska-Guz & Osiejuk 2004, Caro et  
385 al. 2009, Wonke & Wallschläger 2009). It has been shown that these regional song  
386 differences affect the sexual response of females (Baker et al. 1987). Similarly,  
387 ortolan bunting males share final parts of the song, but these elements may have  
388 different acoustical structures (usually they are low frequency, narrowband trills) in  
389 different populations. In the majority of the populations studied thus far, all males  
390 within a local dialect area have a single version of the final structure (review in  
391 Cramp & Perrins 1994 and Osiejuk et al. 2003). Thus, because cinnamon-breasted  
392 bunting songs have a more variable initial song and a fully shared stereotyped whistle  
393 at the end of the song, this finding seems to reflect the same geographical pattern as  
394 other bunting species (i.e., with local dialect and an easy to detect “dialect cue” in a  
395 form of the final whistle). However, the term “dialect” is quite vague. For example,  
396 depending on the form of the final whistle one may distinguish only two large dialect  
397 areas in Europe for the yellowhammer bunting (Cramp & Perrins 1994). However, it  
398 is possible to detect some specific differences at a smaller scale (e.g., Hansen 1985,  
399 Caro et al. 2009, Wonke & Wallschläger 2009). In ortolan buntings, dialects usually  
400 cover smaller areas of hundreds of square kilometres. However, under some specific  
401 ecological conditions this characteristic pattern may completely disappear, as found in  
402 the isolated and patchy population at the border of the species range in Norway  
403 (Osiejuk et al. 2003). In such a population, the final song structures do not act as  
404 dialect cues (Osiejuk et al. 2007a). It is not known whether the final g-whistle is  
405 shared only among cinnamon-breasted bunting males in the studied population or if it  
406 is typical for males from larger areas. Unfortunately, there is a paucity of data, which  
407 hinders further discussion. I did not find such a final whistle in my own recordings  
408 from Lesotho (1998, a few males of subspecies *E. t. tahapisi* recorded, unpubl. data).  
409 There is also no such whistle in songs recorded from Zimbabwe (Macaulay Library  
410 recording #79983, Ethiopia, spp. *tahapisi*; after J. del Hoyo 2005,  
411 [http://ibc.lynxeds.com/video/cinnamon-breasted-bunting-emberiza-tahapisi/bird-rock-](http://ibc.lynxeds.com/video/cinnamon-breasted-bunting-emberiza-tahapisi/bird-rock-singing)  
412 [singing](http://ibc.lynxeds.com/video/cinnamon-breasted-bunting-emberiza-tahapisi/bird-rock-singing)) or Yemen (Poul Hansen, pers. comm.). On the other hand, I was able to  
413 detect final g-whistles in songs of males at a distance of up to 7 km from the study  
414 area and at the altitude of around 1000 m a.s.l., which suggests that the g-whistle  
415 dialect probably is spread over 100 km<sup>2</sup> or more. Additionally, such whistles are  
416 clearly present in recordings of males from the same subspecies in NW Nigeria

417 (Chappuis 2000). These comparisons suggest that the characteristic whistle is  
418 widespread among *E. t. goslingi* populations. The differences in dialect formation  
419 between subspecies may not only be caused by variations in learning patterns and  
420 dispersal strategies (Catchpole & Slater 2008) but may also be due to genetic  
421 differences (Matessi et al. 2000).

422         However, the cinnamon-breasted bunting clearly differed from species in  
423 which all males within a local dialect share the same single song type, like the white-  
424 crowned sparrow (Nelson 2000), or a few song types, such as the corn bunting  
425 McGregor 1980, 1986, Osiejuk & Ratyńska 2003).

426         According to the second aspect of spatial song variation, I found a tendency  
427 for males from local groups (within a radius of  $\leq 500\text{m}$ ) to sing more similar song  
428 types than strangers. If young males learn song during the first months after hatching,  
429 which is typical (Beecher & Brenowitz 2005), the observed song distribution in space  
430 could be due to the dispersal pattern of males being slightly biased towards settlement  
431 within the patch where they hatched. Alternatively, the same result could be obtained  
432 if males tend to settle after dispersal within a group where other males sing similarly.  
433 Whatever the relationship between learning and dispersal is, it should be stressed that  
434 the observed sharing is weak among neighbours within hearing range and within local  
435 groups as a whole. Males sharing the same song type did not aggregate in clusters as  
436 in the corn bunting or the white-crowned sparrow (McGregor, 1980, Osiejuk &  
437 Ratyńska 2003, Nelson 2000).

438

#### 439 *Song post and song rate*

440 Cinnamon-breasted bunting males seemed to be opportunists in the choice of song  
441 posts. They tended to sing from places slightly above the surrounding vegetation but  
442 often did not choose very exposed places. It seems that the males maximised sound  
443 transmission but simultaneously avoided being exposed to others (e.g., conspecifics or  
444 predators). This is quite similar to the behaviour of the ortolan bunting (Tryjanowski  
445 2001). However, it is different from behaviour the of the corn bunting males that  
446 clearly choose the highest possible place (probably because of interactions with other  
447 males, Oliniewicz & Osiejuk 2003) or the yellowhammer bunting males that expose  
448 yellow feathers during singing as a signal of quality to females (Sundberg 1995).

449 Cinnamon-breasted bunting males had quite variable singing rates with mean  
450 values and maxima exceeding those reported for other buntings (e.g., mean = 6.3 (2-  
451 12.4) songs per minute in the yellowhammer, Rutkowska-Guz & Osiejuk 2004; mean  
452 = 4.9 (1.4-10.4) in the ortolan bunting; and mean = 6.2 (3.2-11.1) in the corn bunting,  
453 Olinkiewicz & Osiejuk 2003). Thus the song rate seems to be an important signal in  
454 the cinnamon-breasted bunting, as it is the main song character that may be modulated  
455 during performance.

456

457 In summary, the song of the cinnamon-breasted bunting seems to be an  
458 extremely good model for a large-scale survey due to its moderate structural  
459 complexity, short song duration and single song type per male. It is relatively easy to  
460 obtain recordings of many individuals in a short time. The species is divided into five  
461 clear subspecies, and their populations are fragmented with variable patterns across  
462 Africa (Byers et al. 1995). Therefore, the cinnamon-breasted bunting seems to be a  
463 good model species for the study of interactions between ecology and cultural  
464 transmission of song (Laiolo & Tella 2006).

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- 599



600

601 **Tables**

602 Table 1. Basic parameters of the cinnamon-breasted bunting song from the Bamenda  
603 Highlands.

| Variable                | Minimum | Maximum | Mean±s.d.  | <i>n</i> |
|-------------------------|---------|---------|------------|----------|
| Song duration (s)       | 0.23    | 2.08    | 1.24±0.214 | 1032     |
| Minimum frequency (kHz) | 1.95    | 8.94    | 2.47±0.255 | 1032     |
| Maximum frequency (kHz) | 6.91    | 11.55   | 9.17±0.476 | 1032     |
| Frequency range (kHz)   | 1.28    | 8.97    | 6.70±0.548 | 1032     |

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608 Table 2. Characteristics of the cinnamon-breasted bunting song posts.

| Song post | <i>n</i> | %    |
|-----------|----------|------|
| Ground    | 4        | 7.1  |
| Rock      | 10       | 17.5 |
| Herb      | 4        | 7.1  |
| Fence     | 1        | 1.7  |
| Shrub     | 6        | 10.5 |
| Tree      | 32       | 56.1 |
| Total     | 68       | 100  |

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613 **Tables**

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615 Highlands.

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617 **Figure legends**

618 Fig. 1. Sonograms of the cinnamon-breasted bunting songs with terms used to  
619 describe acoustic song structure and syllable type diversity.

620 Fig. 2. Sonograms of the eight different song types described in the studied population  
621 of cinnamon-breasted bunting from the Bamenda Highlands. Song types are ordered  
622 from “a” to “h” with decreasing frequency as they were found in the repertoires of 58  
623 males (i.e., song type a was sung by 13 males, type b was sung by 11 males, etc.).

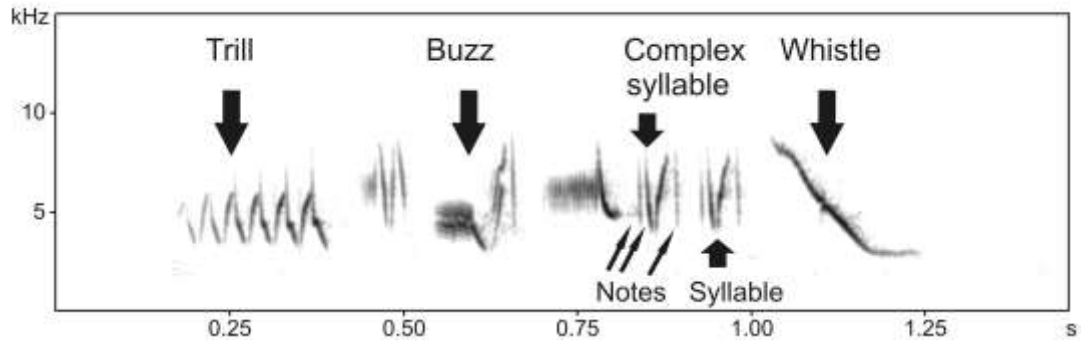
624 Fig. 3. Binary song type sharing among pairs of males (1000 bootstrap) belonging to  
625 three categories: neighbours, local group and strangers.

626 Fig. 4. Song type similarity measured by the Jaccard index among pairs of males  
627 (1000 bootstrap) belonging to three categories: neighbours, local group and strangers.

628

629 **Figures**

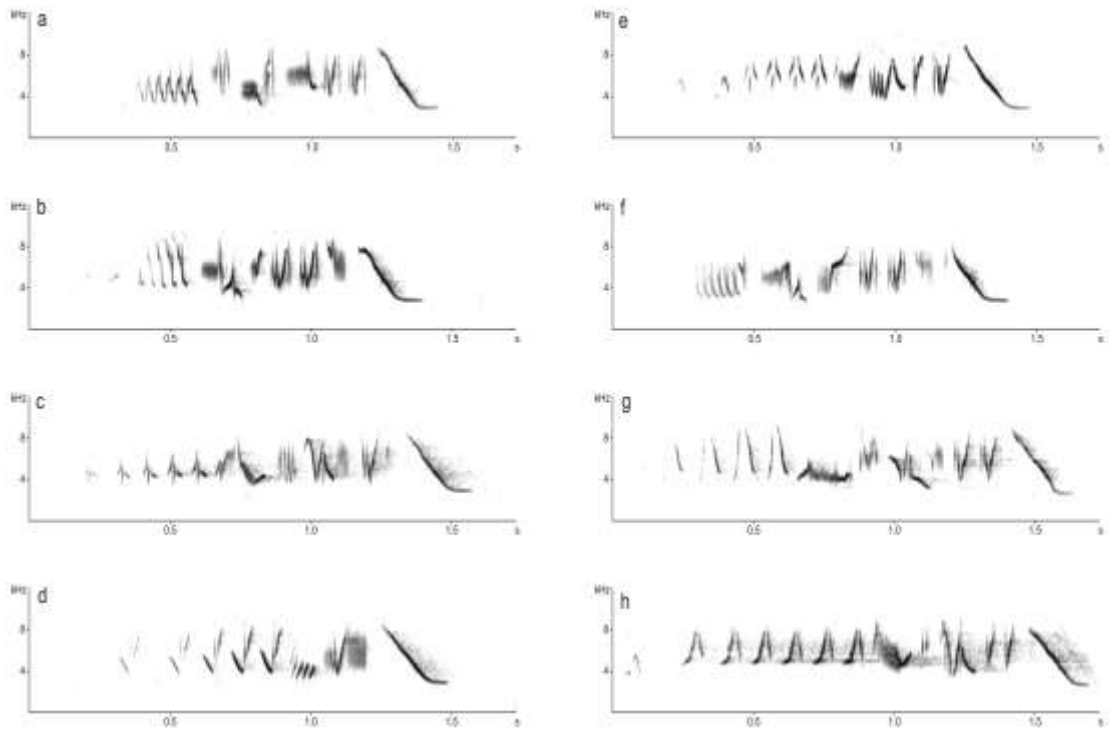
630 Fig. 1



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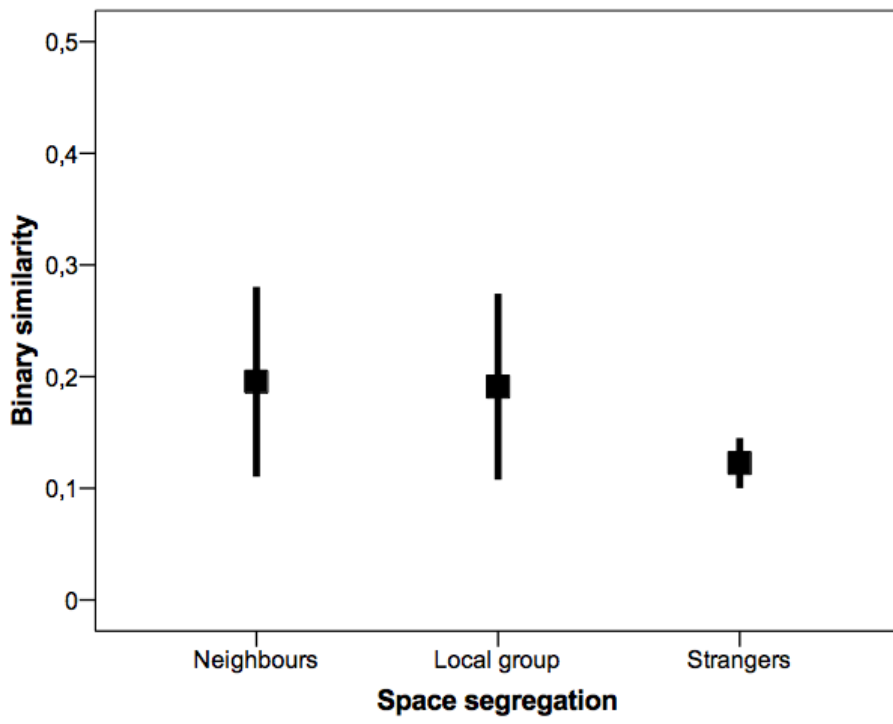
633 Fig. 2



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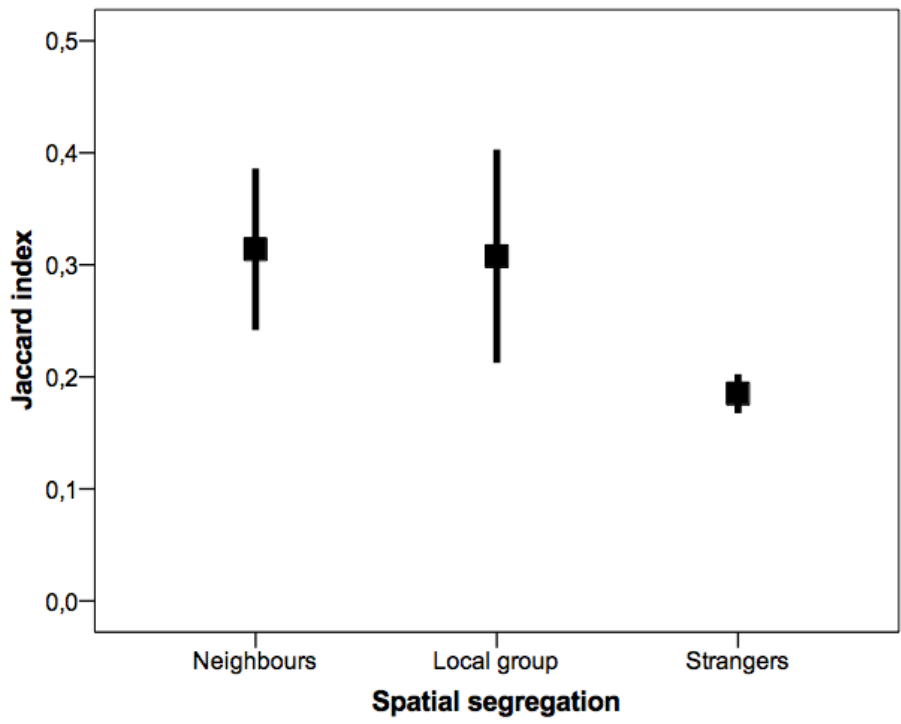
636 Fig. 3



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640 Fig. 4.



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